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BRACONIDAE (HYMENOPTERA) FROM KOREA XX. ALYSIINAE: ALYSIINI, ASPILOTA GENUS-GROUP

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Twenty-one alysiine species are reported from Korea: 11 *Aspilota* species (of which four are new to science) and 10 *Dinotrema* species. The new species are as follows: *Aspilota aestiva* sp. n., *A. latipelus* sp. n., *A. longifemur* sp. n. and *A. semipilosa* sp. n.; the new species are related to their nearest allies. The majority of the known species are new to the fauna of Korea. With 42 original figures.

Key words: Korea, Braconidae, new species, faunistics

INTRODUCTION

A total of twenty-one alysiine species are reported from Korea, the species belong to two genera (in parentheses the respective species number): *Aspilota* (11 species) and *Dinotrema* (10 species). From among the eleven *Aspilota* species four are new to science, their specification is presented in the abstract. The alysiine braconid material of the present account is deposited in the Hungarian Natural History Museum (Department of Zoology), Budapest.

Abbreviations – Ocelli: *OOL* = shortest distance between hind ocellus and compound eye; *POL* = shortest distance between hind two ocelli. – Alar veins of fore wing (ACHTERBERG 1993: 5): *m-cu* = recurrent vein, *1-CU(1)* and *2-CU(1)* = first and second sections of the discoidal vein; *2-SR* = first transverse cubital vein; *3-SR* and *4-SR* = second and third sections of the radial (or marginal) vein.

Collecting data of every known species are given in an abbreviated form, i.e. only the collecting numbers ("No.") are indicated after the species names, the detailed collecting data (name of the Korean localities, time dates etc.) are listed subsequently in the order of their increasing numbers:

No. 13. Prov. South Pyongan (=Phenan): NE outskirts of Pyongyang, 22 May 1970. – Netting in grass along brook and in plants of stream bed.

No. 100. Prov. Kaesong (=Kengi): Bagyon san, Bagyon popo (=waterfall), about 27 km SW from the city Kaesong, 7 June 1970. – Singled from riverside vegetation.

No. 144. Prov. South Pyongan: Pyongyan, Hotel Pyongyan garden, 5–6 August 1971. – Taken with Malaise trap.

No. 145. Prov. South Pyongan: De-sang san, 12 km NE from Pyongyan, 7 August 1971. – Netting in the grass and shrub of a coniferous forest.

No. 153. Same locality as No. 145, 8 August 1971. – Netting the grass and shrub levels of a deciduous-coniferous forest.

No. 193. Prov. Ryang-gang: Hyesan, Hyesan Hotel garden, 23 August 1971. – Taken with Malaise trap.

No. 198. Prov. Ryang-gang: Chann-pay plateau, Samjiyon (=Sam-zi-yon), 1600 m, 25 August 1971. – Singled material on flowers of *Larix–Betula* forest along a road.

No. 206. Same locality as No. 198, 1700 m, 27 August 1971. – Singling in a *Larix–Betula* forest along a pathway.

No. 231. Prov. South Pyongan: Za-mo san, 60 km NE from Pyongyan, 2 September 1971. – Singling in sweet chestnut (*Castanea crenata*) forest in a nature conservancy field.

No. 238. Prov. South Pyongan: Nampo, Mts Guk-san-bong, 10 km NE from the town Nam-po, 5 September 1971. – Netting the grass and bushes of *Castanea–Pinus* wood with oak bushes.

No. 251. Prov. Kaesong: Mts Pakyon, Pakyon popo (=waterfall), 27 km NE from the city Kaesong, 500 m, 9 September 1971. – Netting from bushes, shrubs and grass in deciduous forest in the environs of the waterfall.

No. 257. Same locality as No. 251, garden of Pakyon rest home, 10–12 September 1971. – Taken with Malaise trap.

No. 267. Same as No. 145, 18 July 1975, 17–18h. – Netting the grass and shrub levels of a coniferous wood.

No. 273. Prov. South Pyongan: Nampo, 19 July 1975, 11–13.30h. – Netting in the shrub level of a *Robinia–Castanea* wood.

No. 281. Prov. Ryang-gang: Chann-pay plateau 24 km NW of Samjiyon along the road to Mt. Paekdu (=Pektu-san), 2000 m, 24 July 1975. – Netting in more or less devastated clearings of *Larix–Betula* forest.

No. 282. Prov. Ryang-gang: Chann-pay plateau, Samjiyon, 1700 m, 24 July 1975, 16–18.30h, sunny weather with cloudy sky, 22–24°C. – Netted in shrubby and grass vegetation of a *Larix–Betula* forest.

No. 288. Prov. Ryang-gang: Chann-pay plateau, Mt. Paekdu, Mudo-bong, 2100–2200 m, 25 July 1975, 10–13h, sunny weather with cloudy sky, 23–25°C. – Singled material at the meeting of the upper forest and lower grass vegetation levels.

No. 318. Prov. Gang-von: district On-dzong, Kum-gang san, near Hotel Gosong, 250 m, 5 August 1975, 18–19.30h, 23°C. – Netted in a coniferous–locust tree wood on shrubby and soft-stemmed vegetation.

No. 332. Prov. Pyongan: Desang san, 10 km NE of Pyongyan, 1 July 1977. – Confined and rather stony area. Coniferous wood (*Pinus densifolia*) mixed with some *Acer* sp., undergrowth very spare.

No. 343. Tesson, water basin, about 35 km SW of Pyongyan, 4 July 1977. – In the neighbourhood of a coniferous wood mixed with *Robinia* trees; netted in the grass and shrub levels of the wood.

No. 347. Sa Gam, water basin and inundation area of a river, about 30–40 km N of Pyongyan, 5 July 1977. – In the neighbourhood of mixed coniferous–*Robinia* wood. Netted in the grass and shrubby vegetation (*Salix*) on the bank of a river.

No. 358. Kumgang san, Ruekhaam, about 7 km W of Hotel Kumgang, 11 July 1977. – Taken with Malaise trap set up at a clearing in the forest.

No. 372. Mt. Paekdu (=Pektu-san): wooded environs of the Samjiyon Hotel, 18 July 1977. – Taken with Malaise trap set up about 2 km N of the hotel on the left of the road to the Explosion Lake.

No. 374. Same locality as No. 372, 19 July 1977. – Netted in shrubby and grass vegetation about 16 km E of the hotel, at the edge of a coniferous wood growing on the left side of the road to Musan.

No. 376. Same locality and time-date as No. 374. – Netted in the grass vegetation of the wooded surroundings of Hotel Samjiyon.

No. 380. Mt. Paekdu (=Pektu-san), Mupo, brook Dehongdan, 20 July 1977. – Netted in grass vegetation along the brook.

No. 488. Prov. Kangwon: Kumgang san, 12 October 1978. – Swept material mainly from *Dryopteris*-like species, a rather cold, windy day.

No. 911. Pyongyang City: Deasong san, 15 May 1985. – Warm sunny afternoon with wind.

No. 917. Same locality as No. 911, 16 May 1985. – Warm, sunny forenoon, swept the underwood and shrub vegetation.

No. 951. Prov. Kangwon: Kumgang san, 27 May 1985. – Warm, sunny morning, about 24°C. Sweeping the vegetation along the foot-path from Kumgang-mun Gate to the waterfall of Kuryong.

No. 952. Same locality and time date as No. 951. – Cool afternoon with overcast sky, temperature about 17°C. Sweeping the undergrowth of a mixed forest around the rest house Oe-Kumgang.

ALYSIINAE

ASPILOTA FOERSTER, 1862

Aspilota aestiva sp. n.: for description see p. 5.

Aspilota fuscicornis (HALIDAY, 1838) – Localities: 1 ♀: No. 282. 1 ♂: No. 376. 1 ♀: No. 917. – Female antenna with 15 (1 ♀) and 19 (1 ♀) antennomeres, male antenna with 19 (right antenna) – 20 (left antenna) (1 ♂) antennomeres. – A rather sporadic Palaearctic species, new to the fauna of Korea.

Aspilota inflatitempus FISCHER, 1974 – Locality: 1 ♂: No. 332. – Described from Austria, found in Hungary; new to the fauna of Korea.

Aspilota jabingensis FISCHER, 1976 – Locality: 1 ♂: No. 231. – Described from Austria (Burgenland); new to the fauna of Korea. The Korean male was compared to the male holotype.

Aspilota laevinotum TOBIAS, 1962 – Localities: 2 ♀: No. 318. 1 ♀: No. 358. – Antenna with 15 antennomeres, eye in dorsal view longer than temple, hind femur 4.4 times as long as broad distally. – Described from the European part of Russia (Leningrad region); new to the fauna of Korea.

Aspilota latipelus sp. n.: for description see p. 7.

Aspilota longifemur sp. n.: for description see p. 8.

Aspilota parallela FISCHER, 1976 – Localities: 1 ♂: No. 273. 1 ♂: No. 332. 1 ♀: 347. – Described from Austria; new to the fauna of Korea.

Aspilota semipilosa sp. n.: for description see p. 10.

Aspilota stenogaster STELFOX et GRAHAM, 1951 – Localities: 1 ♂: No. 153. 1 ♂: No. 251. 1 ♀ and 2 ♂: No. 282. 1 ♀: No. 318. 1 ♀: No. 376. – Antenna with 18 (3 ♀ and 1 ♂), 17 (1 ♂) and 16 (1 ♂) antennomeres. – Hitherto known only from England, TOBIAS (1962: 111) reported it from the Leningrad region (European part of Russia) with a question mark. New to the fauna of Korea.

Aspilota variabilis TOBIAS, 1962 – Locality: 1 ♀: No. 144. – Described from the Leningrad Region (European part of Russia); new to the fauna of Korea.

DINOTREMA FOERSTER, 1862

Dinotrema castaneithorax (FISCHER, 1973) ♂ new – Localities: 1 ♀: No. 100. 2 ♂: No. 238. 1 ♀: No. 288. 1 ♂: No. 376. – The two females agree with the description. The male is similar to the female. Antenna with 22 (1 ♂) and 24 (1 ♂) antennomeres. Head in dorsal view 1.8 times as broad as long, eye 1.7–1.8 times as long as temple. First tergite 2.2 times as long as broad behind. – Known from Austria; new to the fauna of Korea.

Dinotrema dimorpha (FISCHER, 1976) – Localities: 1 ♂: No. 145. 1 ♂: No. 374. 3 ♀ + 1 ♂: No. 376. 1 ♂ (in Coll. D.-S. KU, Chinju): Korea, KyongNam Chinju, Chojeon-dong, taken with mercury vapour lamp, 9–10 June 1995, leg. KU. – Antenna with 17 (1 ♀), 19 (1 ♀), 21 (1 ♂) and 25 (1 ♂) antennomeres. Head in dorsal view 1.7–1.8 times as broad as long. First tergite subparallel-sided. The species stands very near to *D. paucicrenis* FISCHER. – Described from Austria, new to the fauna of Korea.

Dinotrema divisum (STELFOX et GRAHAM, 1950) – Localities: 1 ♀: No. 193. 1 ♂: No. 332. 1 ♀: No. 374. 4 ♀: No. 376. 1 ♂: No. 488. – Known from Ireland, England, Scotland, Austria and the European part of Russia; new to the fauna of Korea.

Dinotrema glabrum (STELFOX et GRAHAM, 1951) (= *Aspilota venusta* TOBIAS, 1962 **syn. n.**) – Localities: 1 ♀: No. 231. 1 ♀: No. 257. 3 ♂: No. 267. 1 ♂: No. 332. 1 ♂: No. 343. 1 ♂: No. 372. 1 ♀: No. 376. 1 ♂: No. 952. – Body 1.9 mm long. Antenna with 20 antennomeres. Head in dorsal view twice as broad as long. First tergite clearly twice as long as broad behind. Proportional length of veins *3–SR* : *2–SR* as 2.8–2.9 (2 ♀) and 2.1–3 (8 ♂) times as long as *3–SR*. Body brown, first tergite brownish yellow, legs yellow. – Described from Ireland, reported from Austria (FISCHER 1975: 330) the European part of Russia (Leningrad region); new to the fauna of Korea.

Dinotrema latifemur (FISCHER, 1974) – Localities: 3 ♀: No. 282. 1 ♀: No. 376. – Body 2.1 (2 ♀), 2.5 (1 ♀) and 2.7 (1 ♀) mm long. Antenna with 19 (1 ♀), 20 (1 ♀) and 24 (1 ♀) antennomeres, middle antennomeres 1.8 times as long as broad. Hind femur 3.6 times as long as broad. First tergite 1.9 times as long as broad behind. Body brown to dark brown, first tergite (1 ♀) and legs yellow. – Described from Germany, known from Hungary; new to the fauna of Korea.

Dinotrema occipitale (FISCHER, 1973) – Localities: 2 ♂: No. 273. 1 ♂: No. 282. 1 ♂: No. 332. 1 ♀ + 1 ♂: No. 376. 1 ♂: No. 380. – Body 2.1 (♀) and 1.7–2.1 (♀) mm long. Antenna with 21 (1 ♀) and 21–25 (6 ♀) antennomeres. Head in dorsal view 1.6–1.7 times as broad as long. First tergite 2–2.1 times as long as broad behind. Metasoma as long as mesosoma and head combined, mesosoma in lateral view 1.2 times (female holotype 1.28 times) as long as high. – Described from Austria, reported from China; new to the fauna of Korea.

Dinotrema paucicrenis (FISCHER, 1973) – Locality: 1 ♂: No. 374. – Antenna with 24 antennomeres, eye 1.4 times as long as temple. Head in dorsal view 1.76 times as broad as long. *D. dimorpha* (FISCHER) stands very near to this species. – Described from Austria; new to the fauna of Korea.

Dinotrema semicompressus (STELFOX et GRAHAM, 1949) (= *Aspilota parapunctatum* (FISCHER, 1976)) – Locality: 1 ♂: No. 13. – Described from Ireland, England, Scotland (*semicompressus*) and Austria (*parapunctatum*), known also from Hungary; new to the fauna of Korea.

Dinotrema significarium (FISCHER, 1973) (?=*D. longicarinatum* FISCHER, 1976) – Localities: 1 ♀: No. 206. 1 ♀: No. 281. 1 ♂: No. 282. 2 ♀ + 1 ♂: No. 376. 1 ♀: No. 911. – Antenna with 18–26 antennomeres (1 ♀: 18, 2 ♀: 20, 1 ♀ + 1 ♂: 21, 1 ♂: 24, 1 ♂: 26). First tergite 1.8–1.9 times as long as broad behind. *D. longicarinatum* seems to be conspecific with *D. significarium*. – Known from Austria and Hungary; new to the fauna of Korea.

Dinotrema tauricum (TELENGA, 1935) – Localities: 1 ♀: No. 100. 1 ♂: No. 273. 1 ♂: No. 376. – Body 1.7 (1 ♀) and 1.8 (2 ♂) mm long. Antenna with 18 (1 ♂), 19 (1 ♀) and 21 (1 ♂)

antennomeres, middle flagellomeres as long as broad. Head almost twice as broad as long, eye 1.6 times as long as temple. First tergite 1.2 (1 ♀) 1.5 (1 ♂) and 1.9 (1 ♂) times as long as broad behind. Propodeum of one male (loc. No. 273) uneven along its medio-longitudinal line. – Known from the European part of Russia, Hungary, Austria and China; new to the fauna of Korea.

TAXONOMIC PART

Aspilota aestiva sp. n. ♀
(Figs 1–7)

Material examined (1 ♀) – Female holotype: Korea, Pektu-san, Explosion Lake, 2000–2500 m, netting in grasses, 18 July 1977, leg. O. DELY et Á. DRASKOVITS (No. 369). – Holotype is deposited in the Hungarian Natural History Museum (Department of Zoology), Budapest, Hym. Typ. No. 7941. – Condition of the holotype is fairly good: 1.) distal-posterior part of right fore wing somewhat creased; 2.) left spiracle of the first tergite is somewhat more protruding which seems a teratological aberration, the size and form of the right spiracle is normal.

Etymology. – The species name "aestiva" indicates that the holotype specimen was taken in summer (in July).

Description of the female holotype. – Body 3.5 mm long. Antenna about as long as head, mesosoma and half of metasoma combined and with 20 antennomeres. First flagellomere three times, second flagellomere clearly twice as long as broad apically, further flagellomeres gradually shortening and attenuating so that penultimate flagellomere 1.8 times as long as broad. – Head in dorsal view (Fig. 1) transverse, almost twice as broad as long, temple bulging, i.e. head between temples broader than between eyes, eye as long as temple. OOL three times as long as POL. Tentorial pit touching compound eye. Mandible along its median line 1.5 times as long as broad between teeth 1 and 3, teeth 1 and 3 rounded, tooth 2 pointed, two incisions between teeth relatively deep (Fig. 2). Eye in lateral view 1.9 times as long as wide, temple beyond eye 1.2 times wider than eye (Fig. 3). Head polished, face medially hairy.

Mesosoma in lateral view 1.2 times as long as high. Notaulix indicated by a few hairs on disc of mesoscutum, declivous fore part of mesoscutum hairy, otherwise mesoscutum bald. Mesoscutal dimple absent. Precoxal suture long, wide and crenulate, reaching fore margin of mesopleuron but not reaching middle coxa, hind margin of mesopleuron subcrenulate (Fig. 4). Propodeon with a pentagonal *areola basalis*, along keels widely rugose, otherwise rugo-rugulose to uneven, pair of spiracles somewhat protruding (Fig. 5). Mesosoma polished. – Hind femur 3.6 times as long as broad distally (Fig. 6). Hind basitarsus as long as tarsomeres 2–3 and half of tarsomere 4 combined.

Fore wing as long as body. Second submarginal cell long, *3-SR* 2.1 times as long as *2-SR*, *4–SR* straight and almost three times as long as *3-SR*. Vein *1-2CU(1)* twice as long as *m-cu*.

First tergite (Fig. 7) unusually broad, 1.56 times as long as broad behind, pair of spiracles just beyond middle of tergite, up to spiracles broadening, beyond spiracles parallel-sided, pair of basal keels posteriorly merging into longitudinal unparallel striation, hind fourth of tergite rugo-rugulose. Further tergites polished. Ovipositor sheath as long as first tergite, together with ovipositor somewhat upwards curved.

Head and mesosoma blackish brown, metasoma dark rusty brown. Scape and pedicel yellow, flagellum darkening yellow to blackish brown. Mandible blackish, palpi light yellow. Tegula brownish yellow. Legs yellow. Wings hyaline, veins opaque brownish.

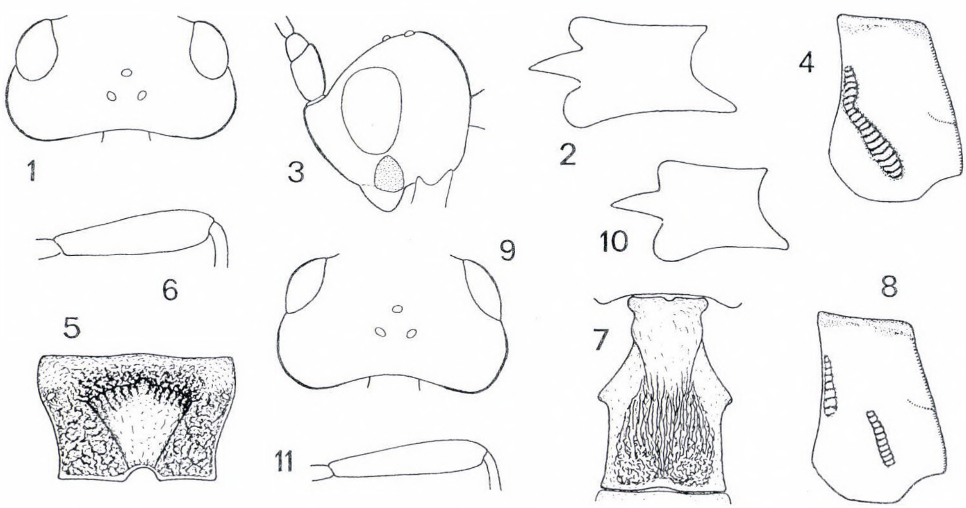
Male and host unknown.

Distribution: Korea.

The new species, *Aspilota aestiva*, runs to *A. delicata* FISCHER, 1973 (Austria, Hungary) with the help of FISCHER's key (1976: 345–357). The two species are distinguished by the following features:

1 (2) Precoxal suture short and narrow, restricted to middle of mesopleuron (Fig. 8). Temple in dorsal view 1.3 times as long as eye. Head 1.7–1.8 times as broad as long (Fig. 9). Mandible 1.4 times as long as broad, incisions between teeth somewhat less deep (Fig. 10). First tergite twice as long as broad behind. Hind femur 4.5 times as long as broad distally (Fig. 11). ♀: 1.8–2.5 mm *A. delicata* FISCHER

2 (1) Precoxal suture long and wide, reaching fore margin of mesopleuron (Fig. 4). In dorsal view temple as long as eye. Head almost twice as broad as long (Fig. 1). Mandible 1.5 times as long as broad, incisions between teeth deeper (Fig. 2). First tergite 1.56 times as long as broad behind (Fig. 7). Hind femur 3.6 times as long as broad distally (Fig. 6). ♀: 3.5 mm **A. aestiva** sp. n.



Figs 1–11. 1–7 = *Aspilota aestiva* sp. n.: 1= head in dorsal view, 2 = mandible with teeth 1 and 3, in full sight, 3 = head in lateral view, 4 = mesopleuron with precoxal suture, 5 = propodeon, 6 = hind femur, 7 = first tergite; 8–11 = *A. delicata* FISCHER: 8 = mesopleuron with precoxal suture, 9 = head in dorsal view, 10 = mandible with teeth 1 and 3 in full sight, 11 = hind femur

Aspilota latipelus sp. n. ♂
(Figs 12–17)

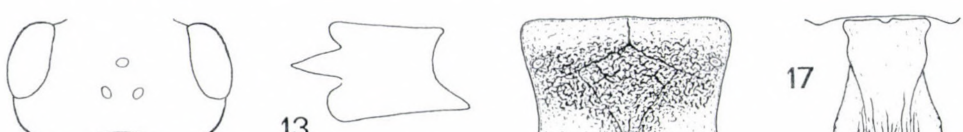
Material examined (1 ♂). – Male holotype: Korea, Prov. South Pyongan, Nam-po, 19 July 1975, leg. J. PAPP et A. VOJNITS (No. 273). – Holotype is deposited in the Hungarian Natural History Museum (Department of Zoology), Budapest, Hym. Typ. No. 7942. – Condition of the holotype is good, left antenna damaged having only 16 antennomeres intact.

Etymology. – The species name "latipelus" is the abbreviated form of latipe[tio]lus and refers to the broad postpetiole.

Description of the female holotype. – Body 2 mm long. Antenna about as long as body and with 21 antennomeres (right antenna). First flagellomere 3.25 times and penultimate flagellomere twice as long as broad, middle flagellomeres 2.7–2.6 times as long as broad. – Head in dorsal view (Fig. 12) 1.9 times as broad as long, eye 1.8 times as long as temple, temple rounded. OOL nearly as long as POL. Tentorial pit touching compound eye. Mandible along its median line 1.4 times as long as broad between teeth 1 and 3, teeth 1 and 3 rounded, tooth 2 pointed, two incisions between teeth fairly deep (Fig. 13). Eye in lateral view 1.55 times as high as wide, temple beyond eye evenly wide and 0.6 times as wide as eye. Head polished, face hairy.

Mesosoma in lateral view stout, 1.2 times as long as high. Middle lobe of mesoscutum hairy, notaulix indicated by a row of hairs. Mesoscutal dimple absent. Precoxal suture short, crenulate-subcrenulate; hind margin of mesopleuron not crenulate. Propodeon rugo-rugulose, pentagonal *areola basalis* less distinct, horizontal base and hind declivous lateral third of propodeon uneven to smooth (Fig. 14). Mesosoma polished. – Hind femur four times as long as broad distally (Fig. 15). Hind basitarsus as long as tarsomeres 2–3 and half of fourth tarsomere combined.

Fore wing somewhat longer than body. Second submarginal cell short, vein *3-SR* 1.8 times as long as *2-SR*, *4-SR* faintly bent and 2.3 times as long as *3-SR*. Vein *1-2CU(1)* 2.4 times as long as *m-cu* (Fig. 16, see arrows).



Figs 12–21. 12–17 = *Aspilota latipelus* sp. n.: 12 = head in dorsal view, 13 = mandible with teeth 1 and 3 in full sight, 14 = propodeon, 15 = hind femur, 16 = veins *1–2CU(1)* and *m-cu*, 17 = first tergite; 18–21 = *A. procreata* FISCHER: 18 = first tergite, 19 = head in dorsal view, 20 = veins *1–2CU(1)* and *m-cu*, 21 = mandible with teeth 1 and 3 in full sight

First tergite 1.4 times as long as broad behind, 1.6 times as broad behind as basally, broadening posteriorly almost gradually, pair of spiracles at its middle, hind part of tergite longitudinally striate and shiny, pair of basal keels merging into striation posteriorly. Rest of tergites polished. Second tergite somewhat longer than third tergite.

Head and mesosoma dark to blackish brown, metasoma brown, first tergite light rusty brown. Palpi pale yellow. Scape, pedicel, tegula and legs yellow. Wings subhyaline, pterostigma brown and veins light brown.

Female and host unknown.

Distribution: Korea.

With the help of FISCHER's key (1976: 353–357) the new species, *Aspilota latipelus*, runs to *A. procreata* FISCHER, 1976 (Austria, Hungary) within the *lobidens* species-group, the two species are distinguished by the following features:

1 (2) Middle lobe of mesoscutum bald. First tergite twice as long as broad behind (Fig. 18). In dorsal view eye as long as temple and head between temples 1.7 times as broad as long, temple faintly bulging (Fig. 19). Antenna with 16–18 (♀) and 18–19 (♀) antennomeres. *1-2CU(1)* 1.5 times as long as *m-cu* (Fig. 20). Two incisions of mandible less distinct (Fig. 21). ♀♂: 1.6–1.8 mm *A. procreata* FISCHER

2 (1) Middle lobe of mesonotum hairy. First tergite as long as broad behind (Fig. 17). In dorsal view eye 1.8 times as long as temple and head 1.9 times as broad as long, temple rounded (Fig. 12). Antenna with 21 antennomeres. *1-2CU(1)* twice as long as *m-cu* (Fig. 16, see arrows). Two incisions of mandible distinct (Fig. 13). ♂: 2 mm **A. latipelus** sp. n.

Aspilota longifemur sp. n. ♀
(Figs 22–26)

Material examined (1 ♀). – Female holotype: Korea, Prov. North Hwanghae, Sinpyong, Pyonghwa-ri, 14 October 1978, leg. A. VOJNITS et L. ZOMBORI (No. 511). – Holotype is deposited in the Hungarian Natural History Museum (Department of Zoology), Budapest, Hym. Typ No. 7943. – The holotype is in good condition, mounted on a pointed card.

Etymology. – The species name "longifemur" refers to the unusually long femora of the species.

Description of the female holotype. – Body 3 mm long. Antenna about as long as body and with 21 antennomeres. First flagellomere four times and second flagellomere three times as long as broad apically, further flagellomeres gradually shortening and attenuating so that penultimate flagellomere 2.5 times as long as broad. – Head in dorsal view transverse (Fig. 22), 1.8 times as broad as long, eye a bit longer than temple, temple rounded. OOL almost twice as long as POL. Tentorial pit touching compound eye. Mandible along its median line 1.7 times as long as broad between teeth 1

and 3, tooth 2 relatively small and pointed, teeth 1 and 3 rounded and tooth 3 larger than tooth 1 (Fig. 23). Eye in lateral view 1.7 times as high as wide, temple beyond eye just shorter than width of eye and ventrally somewhat narrowing. Head polished, face and clypeus hairy.

Mesosoma in lateral view 1.2 times as long as high. Middle lobe of mesoscutum hairy, notaulix indicated by a row of hairs. Mesoscutal dimple absent. Precoxal suture short, crenulate, restricted to middle of mesopleuron; hind margin of mesopleuron not crenulate. Propodeon with a less wide *areola basalis*, propodeon before transverse keel rugulose-uneven, otherwise propodeon uneven to smooth (Fig. 24). Mesosoma polished. – Hind femur five times (Fig. 25), middle femur 5.6 times and fore femur five times as long as broad distally. Hind basitarsus as long as tarsomeres 2–4 combined.

Fore wing about one-fifth longer than body. Vein *3-SR* 2.5 times as long as *2-SR*, *4-SR* faintly bent and 2.3 times as long as *3-SR*. Vein *1-2CU(1)* twice as long as *m-cu*.

First tergite long, 2.6 times as long as broad behind, pair of spiracles at its middle, up to spiracles tergite weakly broadening and beyond spiracles tergite parallel-sided, pair of basal keels meeting before middle of tergite and continuing posteriorly in a median keel, hind half of tergite laterally with a pair of keels, between keels rugulose to uneven (Fig. 26). Further tergites polished. Ovipositor sheath distinctly one-fifth longer than first tergite and curved somewhat upwards.

Scape and pedicel yellow, flagellum darkening brown. Head and mesosoma blackish brown, metasoma dark rusty brown. Palpi pale yellow. Mandible and clypeus brown. Tegula and legs yellow, hind coxa with faint brownish suffusion, distal third of hind tibia brownish. Wings hyaline, veins opaque brownish.

Male and host unknown.

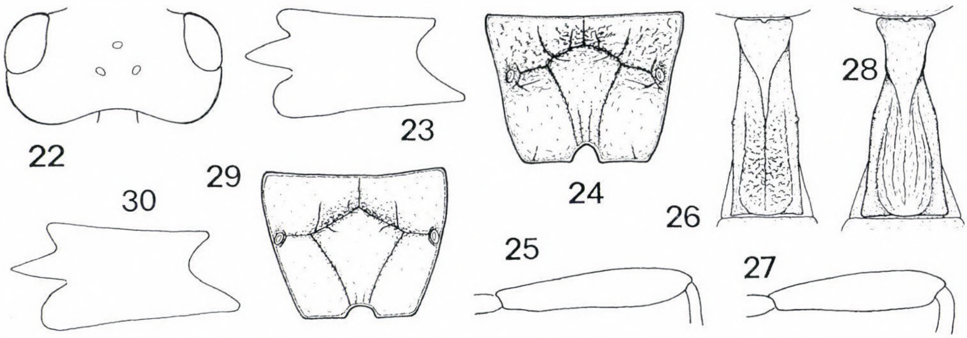
Distribution: Korea.

The new species, *Aspilota longifemur*, runs to *A. fuscicornis* (HALIDAY, 1838) (Palaearctic Region) with the help of FISCHER's key (1976: 345–357), the two species are differentiated by the following features:

1 (2) Middle lobe of mesoscutum bald. Hind femur 4–4.5 times as long as broad distally (Fig. 27). First tergite 2.2–2.4 times as long as broad behind (Fig. 28). Antenna of female with 15–19 antennomeres, penultimate flagellomere 1.8–2 times as long as broad. *Areola basalis* of propodeon wide (Fig. 29). Mandible as in Fig. 30. Flagellomeres 1–2(–3) yellow. ♀: 1.8–2 mm, ♂: 1.7–1.9(–2) mm *A. fuscicornis* (HALIDAY)

2 (1) Middle lobe of mesoscutum hairy. Hind femur five times as long as broad distally (Fig. 25). First tergite 2.6 times as long as broad behind (Fig. 26). Antenna of female with 21 antennomeres, penultimate flagellomere 2.5 times as long as broad. *Areola basalis* of propodeon less wide (Fig. 24). Mandible as in Fig. 23. Flagellomeres 1–2 brown. ♀: 3 mm **A. longifemur** sp. n.

Aspilota longifemur sp. n. is resembling *A. semipilosa* sp. n. by its hairy mesoscutum and long second submarginal cell, however, the two species are clearly distinguished by the following features:



Figs 22–30. 22–26 = *Aspilota longifemur* sp. n.: 22 = head in dorsal view, 23 = mandible with teeth 1 and 3 in full sight, 24 = propodeon, 25 = hind femur, 26 = first tergite; 27–30 = *A. fuscicornis* (HALIDAY): 27 = hind femur, 28 = first tergite, 29 = propodeon, 30 = mandible with teeth 1 and 3 in full sight

1 (2) In dorsal view temple not bulging, i.e. head evenly broad between eyes and temples (Fig. 22). First tergite 2.6 times as long as broad behind, beyond spiracles parallel-sided (Fig. 26). Hind femur five times as long as broad distally (Fig. 25). Teeth 1 and 3 of mandible nearly equal in size (Fig. 23). ♀: 3 mm **A. longifemur** sp. n.

2 (1) In dorsal view temple bulging, i.e. head between temples broader than between eyes (Fig. 32). First tergite twice as long as broad behind, evenly broadening posteriorly (Fig. 37). Hind femur 3.8 times as long as broad distally (Fig. 35). Tooth 3 of mandible larger than tooth 1 (Fig. 33). ♀: 2–3 mm **A. semipilosa** sp. n.

Aspilota semipilosa sp. n. ♀
(Figs 31–38)

Material examined (3 ♀). – Female holotype and two female paratypes: Korea, Prov. Kangwon, Kumgang-san, 12 October 1978, leg. A. VOJNITS et L. ZOMBORI (No. 488). – Holotype and two paratypes are deposited in the Hungarian Natural History Museum (Department of Zoology), Budapest, Hym. Typ. No. 7944 (holotype) and 7945–7946 (paratypes). – The three type specimens are in good condition.

Etymology. – The species name "semipilosa" refers to the anteriorly hairy mesoscutum.

Description of the female holotype. – Body 2.5 mm long. Antenna shorter than body or as long as head, mesosoma and tergites 1–2 combined and with 20 antennomeres. First flagellomere 1.2 times as long as second flagellomere, first flagellomere 2.8 times, second flagellomere 2.3 times (Fig. 31) and penultimate flagellomere twice as long as broad, middle flagellomeres 1.6 times as long as broad. – Head in dorsal view (Fig. 32) 1.8 times as broad as long, temple clearly bulging, i.e. head be-

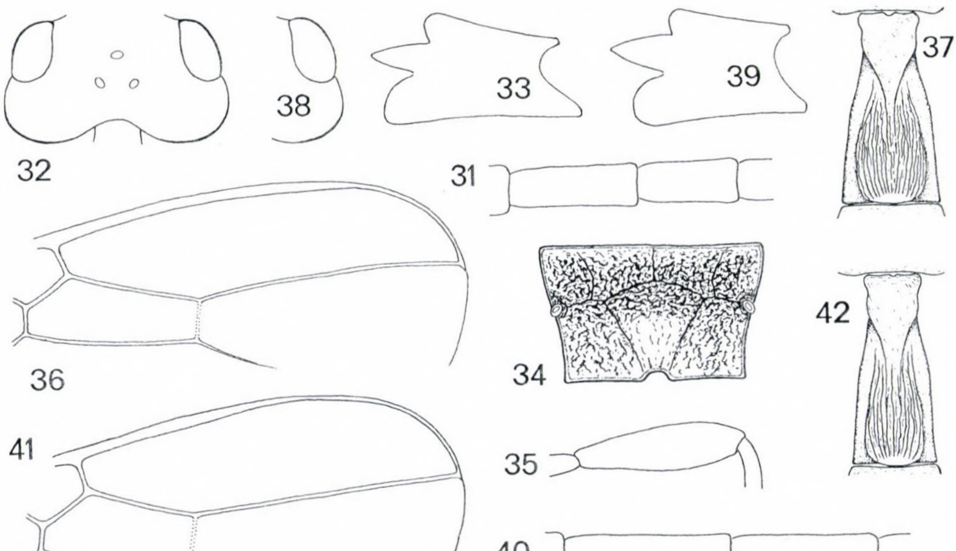
tween temples broader than between eyes, eye slightly (1.1 times) longer than temple, occiput deeply excavated. OOL twice as long as POL. Tentorial pit touching compound eye. Mandible along median line 1.75 times as long as broad between teeth 1 and 3, tooth 2 pointed, teeth 1 and 3 rounded, first (or upper) tooth small and its outer margin almost perpendicular to that of second tooth (Fig. 33). Eye in lateral view 1.7 times as high as wide, temple beyond eye widening ventrally and at its widest part as wide as eye. Head polished, face hairy.

Mesosoma in lateral view 1.2 times as long as high. Anterior half of middle lobe of mesoscutum hairy, notaulix indicated by a row of hairs. Mesoscutal dimple absent. Precoxal suture short, crenulate; hind margin of mesopleuron finely crenulate. Propodeon with a pentagonal *areola basalis*, its surface rugo-rugulose and only hind half of areola smooth and shiny (Fig. 34). Mesosoma polished. – Hind femur 3.8 times as long as broad distally (Fig. 35). Hind basitarsus as long as tarsomeres 2–3 combined.

Fore wing one-fifth longer than body. Vein *3-SR* 2.7 times as long as *2-SR*, *4-SR* faintly bent and twice as long as *3-SR*. Second submarginal cell narrowing distally (Fig. 36). Vein *1-2CU(1)* 2.5 times as long as *m-cu*.

First tergite twice as long as broad behind, moderately and evenly broadening posteriorly, pair of spiracles at its middle, surface of tergite longitudinally striate (Fig. 37). Third tergite somewhat longer than second tergite, tergites polished. Ovipositor sheath longer than first tergite or as long as middle tibia.

Scape and pedicel yellow, flagellum darkening brown. Head and mesosoma blackish brown, metasoma brown, sternites 1–2 with yellowish tint. Palpi pale. Tegula and legs yellow, hind tibia



Figs 31–42. 31–38 = *Aspilota semipilosa* sp. n.: 31 = flagellomeres 1–2 in lateral view, 32 = head in dorsal view, 33 = mandible with teeth 1 and 3 in full sight, 34 = propodeon, 35 = hind femur, 36 = distal part of right fore wing, 37 = first tergite, 38 = right part of head in dorsal view; 39–42 = *A. imparidens* FISCHER: 39 = mandible with teeth 1 and 3 in full sight, 40 = flagellomeres 1–2 in lateral view, 41 = distal part of right fore wing, 42 = first tergite

darkening brown, basally yellow. Tip of fifth tarsomeres darkening. Wings hyaline, pterostigma and veins light brown.

Description of the two female paratypes. – Similar to the female holotype. Body 2 mm (1 ♀) and 3 mm long (1 ♀). First flagellomere 2.8–3 times and second flagellomere 2.3–2.5 times as long as broad apically. Eye in dorsal view 1.2 times (1 ♀) as long as temple, temple a bit less bulging (1 ♀). Propodeon less roughly sculptured (1 ♀). First tergite 1.8 times (1 ♀) and 2.1 times (1 ♀) as long as broad behind.

Male and host unknown.

Distribution: Korea.

The new species, *Aspilota semipilosa*, runs to the *A. fasciatae* species-group (FISCHER 1976: 353) owing to its small first mandibular tooth and is nearest to *A. imparidens* FISCHER, 1974 (Austria, Hungary) considering the corporal size, small first tooth of mandible and dark colour of body; their specific distinction is keyed:

1 (2) Fore half of mesoscutum hairy. Mandible as in Fig. 33, tooth 3 somewhat less rounded. Antenna with 20–21 antennomeres, first flagellomere 2.8–3 times and second flagellomere 2.3–2.5 times as long as broad apically (Fig. 31), penultimate flagellomere twice as long as broad. Vein *3-SR* 2.7 times as long as *2-SR* (Fig. 36). First tergite 1.8–2 times as long as broad and moderately broadening posteriorly (Fig. 37). Ovipositor sheath longer than first tergite or as long as middle tibia. ♀: 2–2.5 mm **A. semipilosa** sp. n.

2 (1) Fore half of mesoscutum bald (only along notaulix with hair-line as usually). Mandible as in Fig. 39, tooth 3 rounded. Antenna with 19 antennomeres, first flagellomere 4.1–4.3 times and second flagellomere 3.7–3.8 times as long as apically broad (Fig. 40), penultimate flagellomere 2.2–2.9 times as long as broad. *3-SR* 1.8–2.1 as long as *2-SR* (Fig. 41). First tergite 2–2.4 times as long as broad and beyond spiracles less broadening (Fig. 42). Ovipositor sheath as long as first tergite. ♀♂: 2 mm *A. imparidens* FISCHER

The new species is also near to *A. insolita* TOBIAS, 1962 (European part of Russia: Saint Petersburg region) considering their common features as propodeon with *areola basalis*, precoxal suture short and eye slightly longer than temple; the two species are distinguished by the following features:

1 (2) In dorsal view temple rounded, head between temples as broad as between eyes. Mesoscutum bald except a row of hairs indicating notaulix. Antenna with 18 antennomeres, middle antennomeres 2.5–3 times as long as broad. Hind femur 4.5–5 times as long as broad distally. Vein *3-SR* 1.6–2 times as long as *2-SR*. Tergites 1–2 yellow to reddish yellow. ♀: 2 mm, ♂: 1.7 mm *A. insolita* TOBIAS

2 (1) In dorsal view temple bulging, head between temples broader between eyes (Fig. 32). Fore half of mesoscutum hairy. Antenna with 21 antennomeres, middle flagellomeres 1.6 times as long as broad. Hind femur 3.8 times as long as broad distally (Fig. 35). Vein *3-SR* of fore wing 2.7 times as long as *2-SR* (Fig. 36). Tergites 1–2 dark rusty brown. ♀: 3 mm **A. semipilosa** sp. n.

*

Acknowledgements – My taxonomic work on the Korean species of *Aspilota* and *Dinotrema* was efficaciously supported by my good friend DR. M. FISCHER (Wien) with his kind permission of a long-termed loan of the type specimens of many *Aspilota* and *Dinotrema* species described by him and, furthermore, by Dr. R. CONTRERAS–LICHTENBERG's hospitality, directress of the 2. Zoologische Abteilung des Naturhistorischen Museums in Wien who kindly arranged my work and lodgement as guest-visitor in her museum for five days in May 2000. My sincere thanks should go to Dr. S. SCHÖDL, curator of the Hymenoptera Section in Vienna Museum who placed at my disposal the facilities needed for my taxonomic work in his section.

REFERENCES

ACHTERBERG, C. VAN (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zool. Verh. Leiden* **283**: 1–189.

CHEN, J. & WU, ZH. (1994) The Alysiini of China (Hymenoptera: Braconidae: Alysiinae). *China Agriculture Press* 178 pp. + 40 tables. [In Chinese with English abbreviated text p. 154–168, key to *Aspilota* species: p.159–160.]

FISCHER, M. (1972) Erste Gliederung der paläarktischen Aspilota-Arten (Hymenoptera, Braconidae, Alysiinae). *Polskie Pismo Entom.* **42**(2): 323–459.

FISCHER, M. (1973) Alysiini aus dem Land Salzburg, gesammelt von Herrn Dr. Paul Babiy (Hymenoptera, Braconidae). *Ann. Mus. Civ. Stor. Nat. Genova* **79**: 235–270.

FISCHER, M. (1974) Einige neue Aspilota-Arten aus Niederösterreich (Hymenoptera: Braconidae, Alysiinae). *Folia ent. hung.* **17**(1): 59–71.

FISCHER, M. (1975) Alysiinen-Wespen aus der Umgebung von Hüttenberg in Kärnten (Hymenoptera, Braconidae, Alysiinae). *Carinthia II* **165/85**: 303–342.

FISCHER, M. (1976) Erste Nachweise von Aspilota-Wespen im Burgenland (Hymenoptera, Braconidae, Alysiinae). *Ann. Naturhist. Mus. Wien* **80**: 343–410.

STELFOX, A. W. & GRAHAM, M. W. R. DE V. (1950) Notes on the genus Aspilota (Hym., Braconidae, Alysiinae) with descriptions of four new species. *Entom. m. Mag.* **85**: 9–13.

STELFOX, A. W. & GRAHAM, M. W. R. DE V. (1951) Descriptions of two new species of Aspilota (Hym., Braconidae) from England. *Entom. m. Mag.* **87**: 222–223.

TOBIAS, V. I. (1962) Contribution to the fauna of the subfamily Alysiinae (Hymenoptera, Braconidae) of the Leningrad Region. *Trudy Zool. Inst.* **31**: 81–137. [In Russian with English title.]

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ORTHEZIOLA OF ASIA WITH THE DESCRIPTIONS OF THREE NEW SPECIES, AND WORLD DISTRIBUTION OF THE GENUS (HOMOPTERA: COCCOIDEA, ORTHEZIIDAE)

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Three new *Ortheziola* species (*O. peregovitsi*, *O. vietnamiensis*, *O. matskasii*) are described from Asia. By these descriptions the number of the known *Ortheziola* species of the World increases to 23. Distribution records and zoogeographical considerations are given. The new species represent a link between the Palaearctic, Oriental and Ethiopian Regions. The records gave a new insight into the species richness of this genus in the World.

Key words: Homoptera, Coccoidea, Ortheziidae, *Ortheziola*, Asia, zoogeography

INTRODUCTION

The genus was analysed in detail by MORRISON (1925, 1952), KOSZTARAB and KOZÁR (1988), KOZÁR (1998), KOZÁR and KONCZNÉ BENEDICTY (1999) and KOZÁR and MILLER (2000), and they found 20 species.

The aim of this work is to continue the study of the genus *Ortheziola*, and to learn more about the distribution patterns of the species.

MATERIALS AND METHODS

This study presents the results of the analyses of 730 samples from throughout Asia. The samples contained 63 females and 65 larvae of Ortheziidae, with 11 females of *Ortheziola* from 6 samples. The descriptions follow the terminology of the different morphological characters as given in the work of KOZÁR and MILLER (2000).

The insects were collected mostly from Berlese funnel samples. The collectors are mentioned in the descriptions. The insects are from the Collection of Arachnida of the Hungarian Natural History Museum, Budapest, Hungary (HNHM). The samples originated from the following countries: Afghanistan, Armenia, China, India, Iraq, Maldive Is., Mongolia, Nepal, Republic of Korea and Peoples Republic of Korea, Russia, Thailand, Ukraine, Vietnam.

The insects including some larval stages are preserved on microscopic slides in the collection of the HNHM.

RESULTS

Ortheziola peregovitsi sp. n.
(Fig. 1)

Material examined: Holotype, female, Republic of Korea, Prov. Cheju, Halla-san National Park, 1300 m above sea level, 30. 10. 1993. Berlese funnel, leg. L. PEREGOVITS (No. 664) (HNHM, Budapest).

Description of adult female. Most of the dorsum covered with wax plates. Only a narrow band of dorsum in the midline is bare, and whitish, segmentation not visible. Mounted specimen (Fig. 1) 1.1 mm long and 0.8 mm wide. Antennae 3-segmented, eye stalks fused with pseudobasal antennal segment, the size of segments in µm: 1st – 102 long and 66 wide; 2nd – 59 and 35; 3rd – 275 and 38. One sensory pore on 2nd segment of the antenna. The 3rd segment almost parallel-sided. Apical seta of antenna 138, subapical seta 48 long. A strong flagellate sensory seta and a microseta are situated near apical seta. The segments of antennae are covered with a few thick setae, 19 long. On first antennal segment of the some setae clavate. Eye stalks elongate, thumb-like.

Venter. Length of body parts in µm: Labium 2-segmented, 140 long. Stylet loop longer than labium. Legs: coxa of anterior legs 112, trochanter-femur 317, tibia and tarsus 349, and claw 49. Coxa of middle legs 128, trochanter-femur 332, tibia and tarsus 349, and claw 49. Coxa of posterior legs 144, trochanter-femur 390, tibia and tarsus 398, and claw 54, claw digitules 13. Claw without denticle. Legs with rows of 17 long thick setae; Tibia with one sensory pore and one 28 long flagellate sensory seta. There are three flagellate setae on end of trochanter-femur. Thoracic spiracle openings with a small marginal group of wax plates, with an additional small group (wax plate no. 17, 18) in front of coxae, too. At margin in front of spiracles a row of pores containing 6 to 9, 4-locular pores, 4 in diameter, and 2 setae on margin. Diameter of anterior spiracles 26. Venter of thorax with a small number of scattered setae, some setae on the margin, around mouth parts and on abdomen clavate. Venter of abdomen with one band of six-locular pores, 6 in diameter in the only one wax plate band in front of vulva. No pores around vulva.

Dorsum. Dorsal wax plates cover most of dorsum. Wax plates situated on margin of bands, spines 13–16 long. Wax plate No. 3 divided (like in *O. britannica*), but both parts well developed. The wax plates Nos. 5, 6 well separated. Some slender setae situated in dorsal plate bands and on bare segments, most of them clavate. Sclerotized anal plate situated in front of anal ring, 35 wide and 198 long, with some seta, some of them clavate. Anal ring destroyed. Diameter of the anal ring 47, seta 38. On both sides of anal ring a group of thumb-like pores (following the terminology given by KOZÁR & MILLER, 2000), 7 long, and a group of 10-locular pores visible. The microtubular ducts (6 µm in diameter) scattered on dorsum, around wax plate bands and on venter. They resemble simple pores. Abdominal spiracles not detectable.

The species is named in honour of L. PEREGOVITS (HNHM, Hungary), in order to acknowledge his help in collecting this insect.

Comments. This species is distinct from other species by having a great number of clavate setae on the dorsum, and by the separated wax plate No. 3.

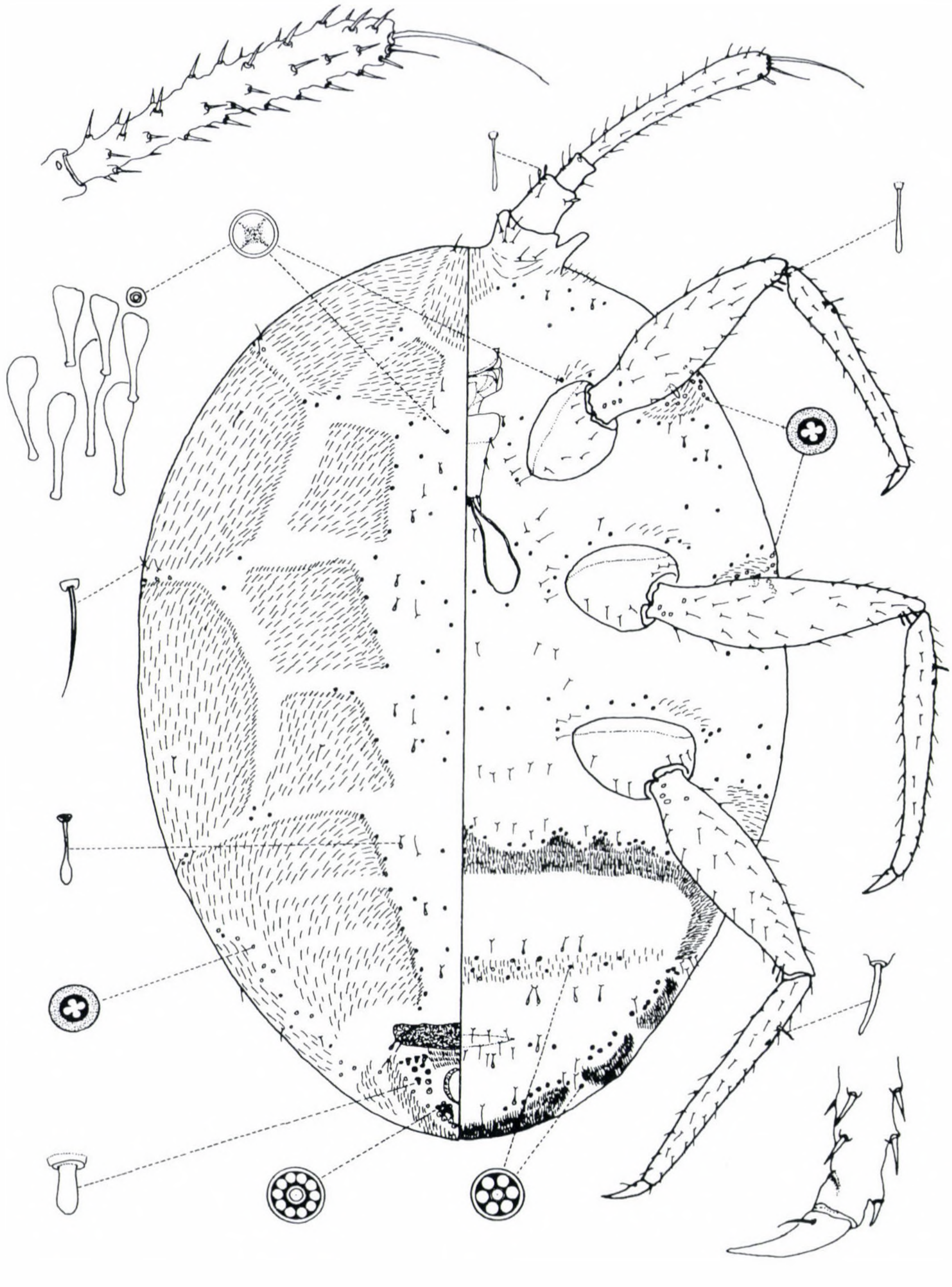


Fig. 1. *Ortheziola peregovitsi* sp. n.

Ortheziola vietnamiensis sp. n.
(Fig. 2)

Material examined: Holotype, female, Vietnam, Da Lat, Thac Datanla waterfall, 1200 m above sea level, 07. 12. 1994. Berlese funnel, leg. S. MAHUNKA (No. 672) (HNHM, Budapest). Paratypes, 2 females from the locality of the holotype. 3 female, Da Lat, Com Ly area, 08. 12. 1994. (No. 677) (HNHM, Budapest).

Description of adult female. Most of dorsum bare, only margin covered with wax plates. Mounted specimen (Fig. 2) 1.26 mm long and 1.15 mm wide. Antenna 3-segmented, eye stalks fused with pseudobasal antennal segment, size of segments in µm: 1st – 95 long and 72 wide; 2nd – 50 and 35; 3rd – 262 and 40. One sensory pore on the 2nd segment of antenna. The 3rd segment is elongated. Apical seta of antenna 262, subapical seta 45 long. Near apical seta a strong flagellate sensory seta, 16 long and a microseta. The segments of the antennae covered with a small number of thick setae, 13 long. Some clavate setae on first segments. Eye stalks elongate, thumb-like.

Venter. Length of body parts in µm: Labium 2-segmented, 163 long. Stylet loop longer than labium. Legs: coxa of anterior legs 102, trochanter-femur 314, tibia and tarsus 315. Coxa of middle legs 109, trochanter-femur 320, tibia and tarsus 332, and claw 50, claw digitules 10. Coxa of posterior legs 128, trochanter-femur 407, tibia and tarsus 382, claw 58 and claw digitules 12 long. Claw without denticle. Legs with rows of 14 long, thick setae, and with one sensory pore and one 20 µm long flagellate sensory seta. Thoracic spiracle openings with a group of wax plates, without additional bands around the coxae. At margin in front of spiracles a small group of four-locular pores present, 6 µm in diameter, and with 3–4 marginal setae. The diameter of anterior spiracles 26 µm. Venter of thorax with a small number of scattered setae and microtubular ducts. Some clavate setae on abdomen. Venter of abdomen with multilocular pores, 10 in diameter (4 to 12-locular in centre with 1–2 pores).

Dorsum. Most of dorsum bare, only margin covered with wax plates. Wax plates Nos. 4–5 and 6–7 are fused. Plate No. 3 absent. The wax plate spines at the margin of the bands are 16–19 long. Some slender setae are in the dorsal plate bands and on the bare segments. The sclerotized anal ring 64 wide and 179 long; plate situated in front of anal ring, with some setae, a few are clavate. Anal ring with an incomplete double row of round pores and with 6 setae longer than length of anal ring. Anal ring 54 wide and 60 long. On both sides of anal ring a group of thumb-like pores (6 µm long) and groups of multilocular pores. Microtubular ducts (6 long) scattered on dorsum around wax plate bands and between plates and on venter. A row of four-locular pores on body margin. Abdominal spiracles not visible.

The species is named after the country of its origin.

Comments. This species is distinct from other species, especially by the fused dorsal wax plates and by the row of the pores on the dorsal margin near to the dorsal wax plates and by the absence of wax plate No. 3.

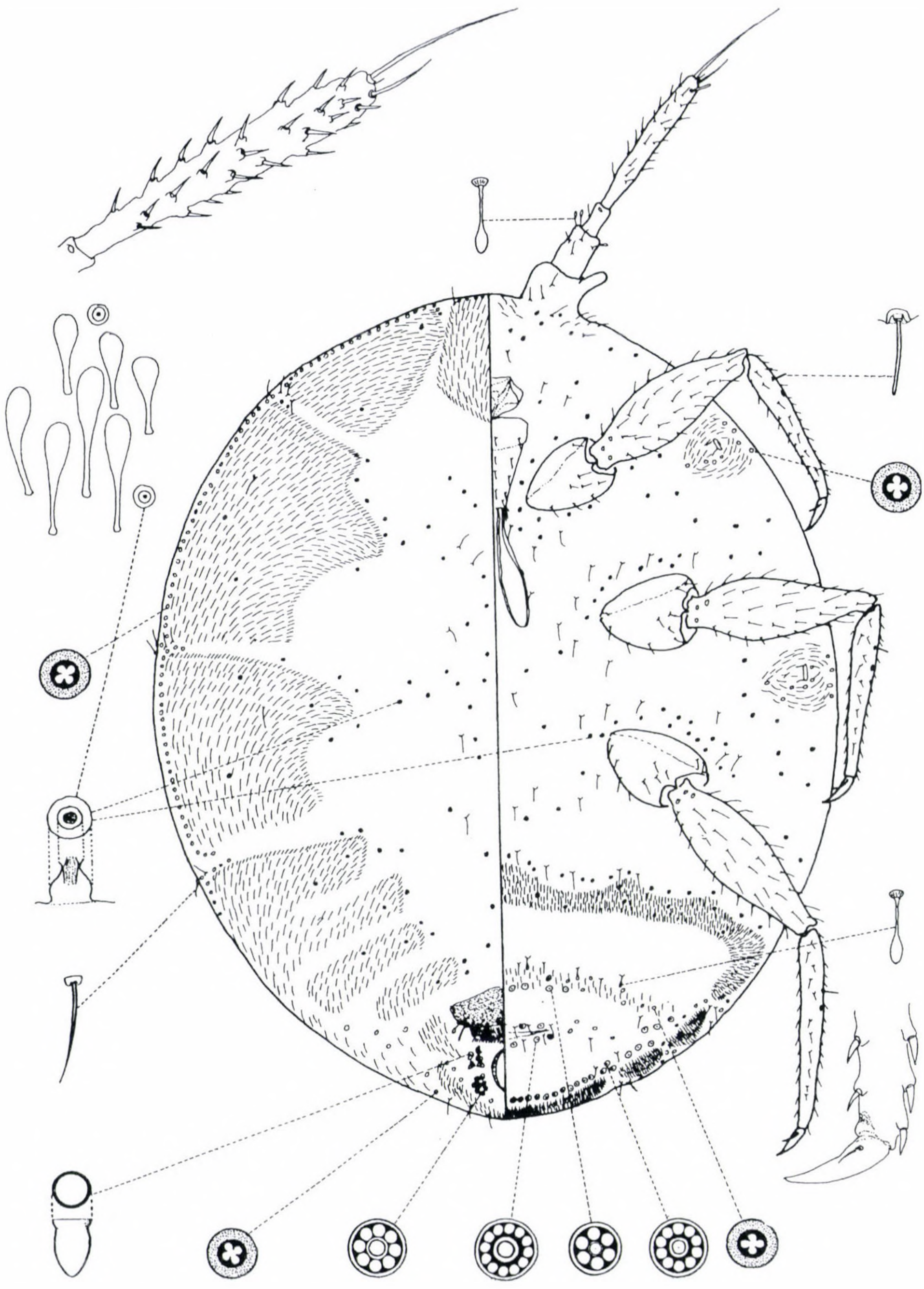


Fig. 2. *Ortheziola vietnamiensis* sp. n.

Ortheziola matskasii sp. n.
(Fig. 3)

Material examined: Holotype, female, Vietnam, O-qui-ho, forest, shifting, 22. 11. 1971 (leg. I. MATSKÁSI and GY. TOPÁL) (No. 252) (HNHM, Budapest).

Description of adult female. Most of the dorsum covered with wax plates. Only a band in midline of dorsum is bare, whitish; no segmentation visible. Mounted specimen (Fig. 3) 1.4 mm long and 1.2 mm wide. Antenna 3-segmented, eye stalks fused with pseudobasal antennal segment, the size of the segments in µm: 1st – 108 long and 70 wide; 2nd – 62 and 48; 3rd – 282 and 51. One sensory pore on 2nd segment of antennae. The 3rd segment not parallel-sided. Apical seta of antenna slender 182 long, subapical seta 32. Near to apical seta a 26 long strong flagellate sensory seta and a microseta present. Segments of antennae covered with thick setae, 18 long, on first segment some clavate setae (Fig. 3). Eye stalks elongate, thumb-like.

Venter. Length of body parts in µm. Labium 2-segmented, 160 long. Stylet loop as long as labium. Legs: coxa of anterior legs 128, trochanter-femur 288, tibia and tarsus 320, and claw 54, claw digitules 12 long. Coxa of middle legs 134, trochanter-femur 314, tibia and tarsus 336, and claw 58. Coxa of posterior legs 153, trochanter-femur 346, tibia and tarsus 416, and claw 60. Claw digitules 14 long. Claw without denticle. Legs with rows of 16 long thick setae, and with one sensory pore and one 24 µm long flagellate sensory seta on tibia. Thoracic spiracle openings with a marginal band of wax plates. On margin in front of spiracles a group of 4-locular pores (7–8) 5 in diameter, and 3–4 setae on dorsal side. Anterior spiracles 26 in diameter. Venter of thorax with a small number of scattered setae and microtubular ducts. Some clavate setae on thoracic margin. Venter of abdomen with 4 to 10 locular pores, in centre with 1–3 pores. Multilocular pores on body margin, four-locular pores in front of the wax plates within ovisac band.

Dorsum. Length of body parts in µm. Dorsal wax plate bands cover most of dorsum. Wax plates Nos. 2–3, 4–5, and 6–7 fused. Wax plate spines 12 long situated at margin of bands, in the middle of the bands 15 long. Some slender setae in dorsal plate bands and on bare segments. Some four-locular pores, 5 in diameter, present in marginal band of abdomen. Sclerotized anal plate situated in front of anal ring, 70 wide and 282 long, with some setae, a few clavate. Anal ring partly destroyed, 46 wide and 49 long. At both sides of anal ring a group of thumb-like pores (6 long) visible. Microtubular ducts (6 in diameter) scattered on dorsum around wax plate bands and between plates on venter. Only first abdominal spiracle visible.

The species is named in honour of Dr. I. MATSKÁSI (HNHM, Hungary) to acknowledge his help in collecting this insect.

Comments. This species is different from others by the absence of multilocular pores around vulva, by the absence of clavate setae on venter and dorsum and by its fused wax plate Nos 2–3.

OTHER STUDIED MATERIALS

Ortheziola vejdovskyi SULC, 1895 was found in western Ukraine, Verecke, 10, 1991, leg. L. RONKAY) (No. 605) (HNHM, Budapest), Armenia (Tsakhkadzor 1800–2300 m above sea level, 01,

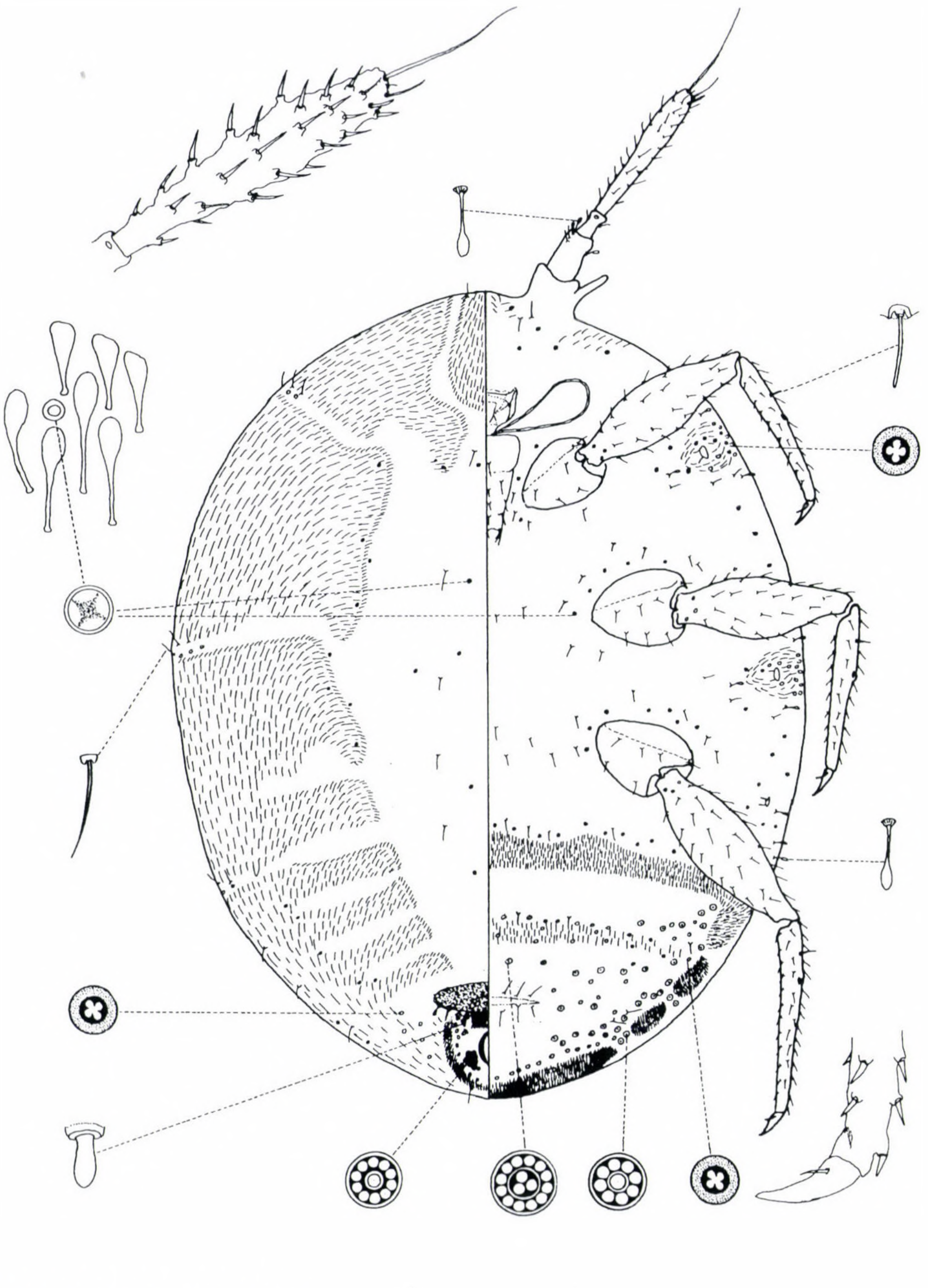


Fig. 3. *Ortheziola matskasii* sp. n.



Fig. 4. Third, or apical segment of all species of the genus *Ortheziola*: a = *O. angolaensis*, b = *O. fercsii*, c = *O. benedictyae*, d = *O. matileferreroae*, e = *O. madecassa*, f = *O. williamsi* g = *O. jermyi*, h = *O. ankazobeensis*, i = *O. kosztarabi*, j = *O. loebli*, k = *O. guineensis*, l = *O. demeteri*, m = *O. szelenyii*, n = *O. vejdovskyi*, o = *O. britannica*, p = *O. saringeri*, r = *O. nellii*, s = *O. mahunkai*, t = *O. ethiopiensis*, u = *O. giliomeei*, v = *O. peregovitsi*, z = *O. vietnamiensis*, x = *O. matskasii* (after KOZÁR & KONCZNÉ BENEDICTY, 1999 with additions)

10. 1982, leg. O. MERKL) (No. 569) (HNHM, Budapest), and in China (Ming Tombs, near to Peking, 19. 09, 1986, leg. B. NAGY) (No. 545) (HNHM, Budapest). This species is new for China, and it is the most eastern record of this species in the Palaearctic Region.

Ortheziola loebli RICHARD, 1990 (?). Second instar larva was found in Nepal (Godawari, 1600 m above sea level, 31. 03, 1984, leg. I. LÖBL.), (No. 512) (HNHM, Budapest). It is important to notice that this larva is from the paratype series of the species, so we can suppose that this larva belongs to this species. Only larval stage was found, which possesses the unique character of *O. loebli* (which is the only species from this group of *Ortheziola*) in the Indian subcontinent.

CONCLUDING REMARKS

The two new species from Southeast Asia (*O. vietnamiensis*, *O. matskasii*) are similar to the four Palaearctic species (*O. britannica*, *O. peregovitsi*, *O. szelenyii*, and *O. vejdovskyi*) possessing only one wax plate row inside of the ovisac band, forming a separate group according by this character. *O. loebli* from Nepal with *O. kosztarabi*, and *O. guineensis* from the Ethiopian Region have also a very special character (wax plates on middorsum), forming another separate group. All the other species from the Ethiopian Region form a third group, however, this group is not totally homogenous, because the setae on the antennae and legs are in some species spiniform, and in others setiform, while in some species are intermediate.

Figure of the 3rd antennal segment is given for all known species. The antennae of the species of this genus look very different in shape, size and setae (Fig. 4). Some species especially differ with long hair-like setae. More details are given for the rest of the species by KOZÁR (1998), KOZÁR and KONCZNÉ BENEDICTY (1999), and KOZÁR and MILLER (2000).

According to the data presented in this contribution and from earlier records, most of the *Ortheziola* species (16) are from the Ethiopian Region (Fig. 5), and they are mostly from the eastern part of Africa. This region appears to be favourable place as a secondary center for the diversification of this genus. Only three species are known from the Oriental, and four from the Palaearctic Region. Surveying the members of the Ortheziidae family, altogether about 3.100 samples were analysed from different parts of the World. In the material from the Neotropics (660 samples), Australia (100 samples), and the Pacific (170 samples) no representatives of the genus *Ortheziola* were found.

In the studied samples (730) from Asia in 4 samples 6 females of *Arctorthezia*; in 8 samples 13 females of *Nipponorthezia*; in 15 samples 33 females of *Newsteadia*; and in 6 samples (6.3%) 11 females of *Ortheziola* were found. Ortheziidae were found in 70 samples (9.6% of the samples). In Africa (1411 samples) (KOZÁR & MILLER 2000) 84 samples (6.0%) contained *Ortheziola* species, but with a much

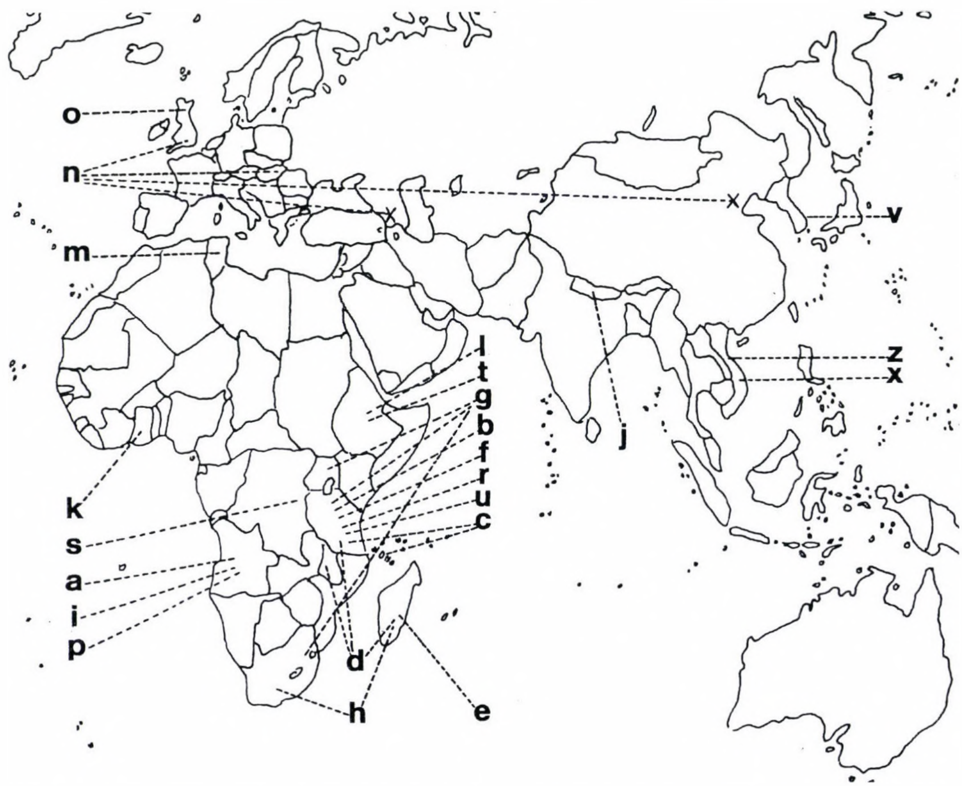


Fig. 5. Distribution of the species of *Ortheziola* in the World: a = *O. angolaensis*, b = *O. fercsii*, c = *O. benedictyae*, d = *O. matileferreroae*, e = *O. madecassa*, f = *O. williamsi*, g = *O. jermyi*, h = *O. ankazobeensis*, i = *O. kosztarabi*, j = *O. loebli*, k = *O. guineensis*, l = *O. demeteri*, m = *O. szelenyii*, n = *O. vejdovskyi*, o = *O. britannica*, p = *O. saringeri*, r = *O. nellii*, s = *O. mahunkai*, t = *O. ethiopiensis*, u = *O. giliomeei*, v = *O. peregovitsi*, z = *O. vietnamiensis*, x = *O. matskasii* (after KOZÁR & KONCZNÉ BENEDICTY, 1999 with additions)

higher number of species. Ortheziidae were found in 121 samples (8.6% of the samples). Pseudococcidae were found in 72, Coccidae in 8, and Diaspididae in 3 samples. All scale insects (Coccoidea) from this survey, excepting the genus *Ortheziola* (Ortheziidae), need further studies.

With this paper we completed a series of work (KOZÁR 1998, KOZÁR & KONCZNÉ BENEDICTY 1999, KOZÁR & MILLER 2000) regarding the World revision of the genus *Ortheziola*. In these papers 18 new species were described. Now the genus contains 23 species. The *Ortheziola* became the second largest in the Ortheziidae family, after the genus *Orthezia* (64 species). The total number of species in the family now increased to 122.

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REFERENCES

KOSZTARAB, M. & KOZÁR, F. (1988) *Scale Insects of Central Europe*. Akadémiai Kiadó, Budapest, 456 pp.

KOZÁR, F. (1998) Ortheziola saringeri sp. n. (Homoptera: Coccoidea, Ortheziidae) from Africa. *Acta Phytopath. et Entomol. Hung*. **33**: 319–323.

KOZÁR, F & KONCZNÉ BENEDICTY ZS. (1999) Ortheziola (Homoptera: Coccoidea) of Africa with descriptions of new species. *Acta Phytopath. et Entomol. Hung*. **34**: 127–136.

KOZÁR, F. & MILLER D. R. (2000) World revision of the genus Ortheziola Sulc, 1895 (Homoptera: Coccoidea) with descriptions of eleven new species. *Systematic Entomology* **25**: 15–45.

MORRISON, H. (1925) Classification of scale insects of the subfamily Ortheziinae. *J. Agricult. Res.* **30**: 97–154.

MORRISON, H. (1952) Classification of the Ortheziidae. Supplement to classification of scale insects of the subfamily Ortheziinae. *USDA, Technical Bulletin* **1052**: 1–80.

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The oribatid species described by Berlese (Acari)

MAHUNKA, S. and L. MAHUNKA-PAPP

The authors had the opportunity for years to study the Oribatid species described by Berlese currently deposited in the Istituto Sperimentale per la Zoologia Agraria at Florence. The results of this series of studies are summarized in this volume.

The volume begins with an essay-like Introduction heavily relying on subjective opinions discussing the general questions of Oribatology. The following section lists Berlese's species placed in the modern system helping the specialists with morphological notes and many drawings; here also the condition of the specimens is discussed and lectotypes are designated.

The third, large section is the catalogue proper, wherein all the species are listed in the systematic order together with their combination and synonymic names. Here one may find all the literature data, usually missing from ordinary works, with reference to Description and Taxonomy, Distribution, with special emphasis on Catalogues whose references are partly unreliable. Where it was deemed necessary further information are added under the heading of Remarks. The volume closes with a very detailed list of literature.

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TAXONOMIC STUDIES ON THE EURASIAN THYATIRIDAE. REVISION OF WERNYA YOSHIMOTO, 1987 GENERIC COMPLEX AND THE GENUS TAKAPSESTIS MATSUMURA, 1933 (LEPIDOPTERA)

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The present paper contains the revisions of the genus *Wernya* and the closely related two new genera, *Hiroshia* gen. n. and *Chiropsestis* gen. n. and the genus *Takapsestis* (s.l.) A new subgenus of *Takapsestis*, *Neotakatogaria* subgen. n., six new species (*Wernya sechuana*, *W. witti*, *W. karsholti*, *W. griseochrysa*, *Chiropsestis rubrocinerea* and *Hiroshia albinigra* spp. n.), and three new subspecies (*Wernya thailandica pallescens*, *Takapsestis (T.) wilemaniella continentalis* and *T. (T.) wilemaniella plumbeata* sspp. n.) are described. The taxonomic stati of certain taxa are revised, *Neogaurena* ROEPKE, 1944, is interpreted as a subgenus of *Takapsestis*, *Wernya baenzigeri* YOSHIMOTO, 1996, is considered as a species distinct from *W. solena* (SWINHOE, 1894); *Takapsestis (Neogaurena) sumatrensis* (GAEDE, 1930) is downgraded to a subspecies of *T. (N.) semiobsoleta* (WARREN, 1915). Three new synonymies are established, *Takapsestis (T.) nepalensis* YOSHIMOTO, 1992 and *T. (T.) harutai* YOSHIMOTO, 1994, are synonyms of *T. (T.) bifasciata* (HAMPSON, 1895); while *T. (T.) griseata* (WARREN, 1915) is conspecific with *T. (T.) orbicularis* (MOORE, 1888). With 89 figures.

Key words: Thyatiridae, new taxa, Himalayan winter and early spring fauna

INTRODUCTION

The exploration of the Lepidoptera fauna of the wide sense Himalayan–Sino–Pacific region has been intensified for the last three decades, the northern parts of Indochina were also targeted lately. The most recent studies were concentrated especially to the mostly neglected late autumnal, winter and early spring aspects.

The above mentioned expeditions collected also a large and diverse Thyatiridae material in the same aspects and habitats. The taxonomic and biogeographical treatment of this vast material revealed the urgent need of the critical revision of our knowledge about the eastern and south-eastern Asian taxa of the family.

The characteristic groups of this winter Thyatiridae fauna, belonging to the tribes Polydactylini and Demopsestini, display strong parallelism with the typical winter Noctuidae fauna in their bionomics, habitat selection and distribution pattern as well. It was highly predictable that at least a part of the Polydactylini and

Demopsestini fauna had undergone similar processes of speciation therefore their species number will increase during the treatment of the recent materials. One of the major aims of our investigations was the testing of this hypothetic fauna-genetical process.

The present paper contains the revisions of two generic groups (one from Polydactylini, another from Demopsestini), which demonstrate the scale of changes, including the increase of the species richness and the range of variation of the formerly poorly known species.

Our studies are based on the Himalayan, Chinese, Indo-Chinese and Taiwanese expedition materials of the Witt Museum, Munich, the Hungarian Natural History Museum, Budapest, and the Zoological Museum of the University of Copenhagen.

The results are summarized in the systematic part of the paper; the critical review of the literature dealing with the given group is discussed in detail in the "History" chapter of each genus.

Abbreviations – BMNH – The Natural History Museum, London; LG – slide of LÁSZLÓ GYULA; RL – slide of RONKAY LÁSZLÓ; HNHM – Hungarian Natural History Museum, Budapest; ZFMK – Zoologisches Forschunginstitut und Museum Alexander Koenig, Bonn; ZMC – Zoological Museum of the University, Copenhagen; ZSM – Zoologische Staatssammlung, Munich; W – slide of the Witt Museum, Munich.

SYSTEMATIC PART

1. THE *WERNYA* GENERIC COMPLEX

Wernya YOSHIMOTO, 1987

Wernya YOSHIMOTO, 1987, *Tyo Ga* **38**(1): 39. Type-species: *Palimpsestis lineofracta* HOULBERT, 1921. Type-locality: China, Ta-tsien-lou.

History. The genus *Wernya* was erected by YOSHIMOTO (1987) during the revision of the *Mimopsestis* MATSUMURA, 1921 (s. l.) species-complex and most of the known species were also described in this work. A part of the Polydactylini genera and their species are discussed in detail in his papers (1983, 1987, 1995), the *Wernya*-like species discovered during the last expeditions to SE Asia originate, however, usually from other parts of this vast biogeographic region. As a result of the studies it was pointed out that there are numerous, externally often confusingly similar, but by their genitalia easily separable, allopatric species.

The externally rather similar *Wernya*-like species show a rather strong segregation, forming three major phyletic lines, which are considered here as different genera, *Wernya*, *Hiroshia* and *Chiropsestis*. These three genera, together with *Mimopsestis*, form a rather compact phyletic line within the tribe "Polydactylini". The newly described genera are yet monotypical since *Wernya* is rather rich in species. It contains 10 species belonging to six different phyletic lineages, which are interpreted as species-groups. The known species of a certain species-group appear as allopatric, while species of different species-groups may occur sympatrically in Indochina (Vietnam, Thailand), together with the species of the related genera *Hiroshia* and *Chiropsestis*. On the basis of the species richness of Polydactylini found in the Indo-Chinese area (especially in the Fan-si-pan Mts) and the large, still unexplored mountainous territories of this region, the discovery of additional new taxa is highly predictable.

Diagnosis. According to our recent knowledge the *Wernya–Mimopsestis* generic complex contains about ten closely related genera, six of them are discussed here as follows: *Wernya* YOSHIMOTO, 1987 (type species: *lineofracta* HOULBERT, 1921), *Mimopsestis* MATSUMURA, 1921 (= *Spilobasis* HOULBERT, 1921; type species: *basalis* WILEMAN, 1911), *Camptopsestis* YOSHIMOTO, 1983 (type species: *malayanus* YOSHIMOTO, 1983), *Polydactylos* MELL, 1942 (type species: *aprilinus* MELL, 1942) and two newly established genera, *Hiroshia* gen. n. (type species: *albinigra* sp. n.) and *Chiropsestis* gen. n. (type species: *rubrocinerea* sp. n.). The external appearance of the species of *Wernya*, *Hiroshia* and *Chiropsestis* are highly similar, except the structure of the last abdominal segment of the female, which is smaller, simple, smooth in *Hiroshia* but much broader, strongly folded in *Wernya*, especially the tergite, bearing a huge tuft of long hairs. The possible function of this tuft is, similarly to other lymantriid and noctuid groups, the covering of the freshly laid eggs, protecting them against the predators. The forewing pattern of *Mimopsestis* is rather different from those of *Wernya*, *Hiroshia* and *Chiropsestis*, displaying stronger similarity with the taxa of *Camptopsestis* and *Polydactylos*.

The genital structure of the closely related genera, *Wernya*, *Hiroshia*, *Chiropsestis*, *Mimopsestis*, *Polydactylos* and *Camptopsestis*, show a different picture, although it is worth to mention that five of the six genera appear as monotypical and the species groups of *Wernya* are also often conspicuously different in some features of the genitalia.

Wernya is rather distant from its relatives by its much robust, compact male genital capsula with strong, often laminate, slightly or strongly bifid uncus, heavily sclerotized, usually bifid, trifid or chelate socii (although a simple, straight socius

may also appear, in the *thailandica*-group), a long, claw-like process of the transtilla can also be found (*griseochrysa*-group). The species of *Wernya* have relatively small, elliptical-rounded valva, most often with smooth surface, although a harpe-like process (*thailandica*-group) or a large, apically acute lobe (*griseochrysa*-group) may be present. The saccular part of the valva is small, narrow, with weak or stronger distal lobe. The configuration of the aedeagus and the vesica is rather constant within the species-groups: longer, tubular, with hooked carina, vesica small, membranous with scobinate basal plates (*lineofracta*- and *rufifasciata*-groups); shorter, thicker with double ventral process of carina, vesica medium-large, inflated, membranous (*thailandica*-group); or thick, short, with simple, slightly hooked ventral process of carina, vesica broad with rather large field of strong, chevron-like cornuti (the *solena*- and the *griseochrysa*-groups). The female genitalia of all known groups of *Wernya* can be characterized by the very compact, strongly sclerotized ovipositor forming a firm cone, the other parts of the apparatus are weakly membranous, a small signum may be present.

The genus *Hiroshia* has long, slender, simple uncus and short, acute, cuneiform socii, rather weak, T-shaped fultura superior, relatively large, broad, subdeltoidal valva with membranous basal and sclerotized distal part, fused with saccular part. The apex of the valva is elongate, the ventral surface with long, acute medial and much shorter ventral processi. Aedeagus rather short, thick, carina with hooked ventral process, tip of hook directed ventro-laterally. Vesica broad, upturned dorsally, medial third armed with large, quadratic field of acute cornuti, this field continuing terminad in narrow ribbon of minute spiculi. In the female genitalia the ovipositor is membranous, setose, without sclerotized plate, the ostial part is very large, granulosely sclerotized, more or less U-shaped, the distal part of the corpus bursae is equipped with scobinate folds and with sclerotized crest, the short medial part is membranous, and the proximal part is large, discoidal, with rather large, lanceolate signum.

In the case of *Chiropsestis* the uncus is simple, slender, with rounded basal plate on ventral side, the socii are short, acute, the fultura superior is reversed T-shaped, with bifurcate dorsal part. The valvae are broad, apically pointed, the apical part is wrinkled, finely hairy, without extensions on ventral surface, contrarily, the saccular part is broad, with two acute terminal extensions. The aedeagus is thick, the ventral process of carina is not hooked, but beak-shaped, the vesica is long, slightly bilobate, broad, inflated, and is armed with a huge field of strong, thick spines and denticles.

The male genitalia of *Mimopsestis* can be characterized by the simple, distally dilated uncus, short but broad, carinate socii, bilobate, dorsally bifurcate fultura superior, broad, distally dilated valva with sclerotized, strong costa, large,

rounded costal lobe and well-developed saccular part with large apical crest. The aedeagus is very long, tubular (the longest within the genus-group), the vesica is very small, membranous, the units of the cornuti field are fused into a sclerotized, serrate plate. The unique feature of the female genitalia is the bilobate, sclerotized papillae anales. The ventral plate between the papillae is sclerotized, trigonal, the penultimate segment is membranous, the dorsal part is narrow, sclerotized, half-ring-like. The ostial part is huge, sclerotized, infundibuliform, the ostium bursae is fused with the short, crest-like, sclerotized ductus bursae; the distal part of the corpus bursae is long, narrow, tubular, the signum is long, rather strong.

The diagnostic features of the male genitalia of *Polydactylos* are the long, sclerotized transtilla with numerous fine, finger-like processi terminad, the thick, straight, apically finely incised uncus, the large sclerotized plate of the ventral surface of the valva, with two long but narrow ventral crests, the very narrow saccular part with fine, triangular distal lobe, the narrow, tubular aedeagus with short, rather weak hook-like process of the carina and the narrowly tubular vesica with small, narrow field of minute spiculi.

The male clasping apparatus of *Camptopsestis* is also rather complex: tegumen characteristically enlarged, robust, heavily sclerotized, with folded ventro-apical lobes. Uncus broad, flattened, triangular, slightly constricted medio-laterally. Socii short, straight, sclerotized, with serrate tips. Fultura superior broad, rugose, with sclerotized-spinulose medial lobes (like in the noctuid genus *Estagrotis* NYE, 1975). Valva short, more or less triangular with apex pointed, ventral surface densely setose. Costa sclerotized, medial crest strong, bar-like, transtilla with huge, flattened, hook-like process at base of valva. Ventro-medial portion of valva with large, cristate-folded, apically dentate lobe extending towards distal end of narrow, short sacculus. Aedeagus rather short, tubular, ventral hook of carina small, weak, its tip directed forward. Vesica projected ventro-laterally, narrowly tubular, membranous, slightly dilated at middle, bearing tiny dorsal diverticulum and small ventral patch of spiculi. The caudal part of the female abdomen is rather acute, covered with smooth hair-scales. In the female genitalia the ovipositor is conical, the papillae anales are rather weak, densely setose, with large, sclerotized, finely dentate and folded ventro-lateral plates; posterior gonapophyses short, weak. Ventral surface of the penultimate segment is membranous, finely wrinkled, dorsal surface with large, sclerotized, butterfly-shaped plate at middle; anterior gonapophyses very long, sclerotized, stick-like. Ostium and ductus bursae small, weak, membranous, the ductus-like posterior part of corpus bursae is very narrow and long, membranous, proximal part of corpus bursae spacious, elliptical-globular, membranous with very fine scobination; signum absent.

Synopsis of the genus *Wernya* YOSHIMOTO, 1987

lineofracta-group

sechuana **sp. n.** Type-locality: China, Sechuan, Daliang Shan.
lineofracta (HOULBERT, 1921). Type-locality: [China], Ta-tsien-lou.
witti **sp. n.** Type-locality: Northern Vietnam, Fan-si-pan Mts.
karsholti **sp. n.** Type-locality: Thailand, Chieng Mai, Doi Inthanon.

rufifasciata-group

rufifasciata YOSHIMOTO, 1987. Type-locality: Taiwan, "Lantou Shein"

thailandica-group

thailandica thailandica YOSHIMOTO, 1987. Type-locality: Thailand, Chiang Mai.
thailandica pallescens **ssp. n.** Type-locality: N-Vietnam, Fan-si-pan Mts.

solena-group

solena (SWINHOE, 1894). Type-locality: [India, Assam] Khasia Hills.
baenzigeri YOSHIMOTO, 1996, **stat. n.** Type-locality: Thailand, Prov. Loei, Phu Luang.

punctata-group

punctata YOSHIMOTO, 1987. Type-locality: Malaysia [Cameron Highland], Tanah Rata.

griseochrysa-group

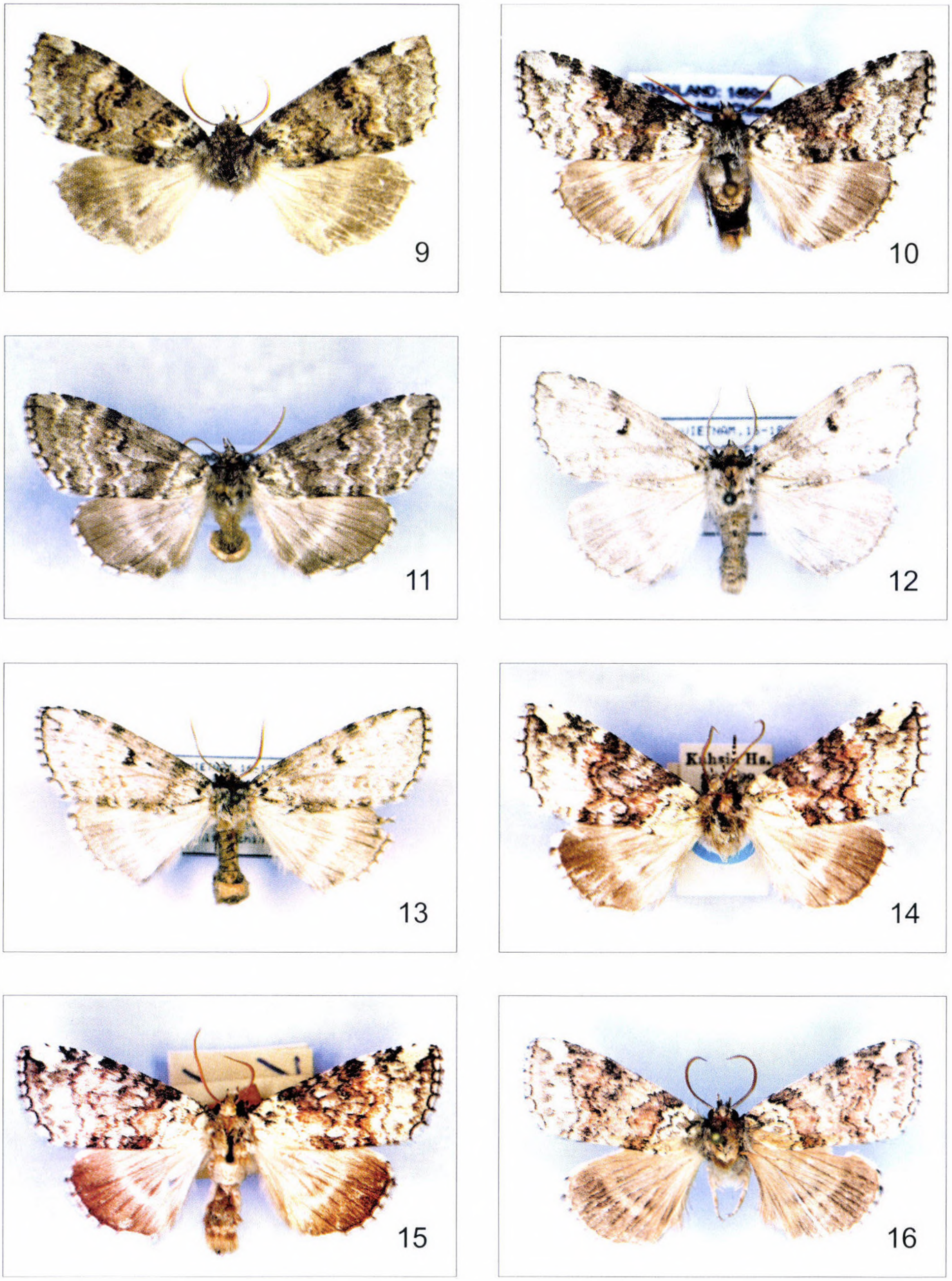
griseochrysa **sp. n.** Type-locality: North Vietnam, Tam Dao.

Bionomics. The species inhabit mountainous deciduous forests, most often at medium high altitudes. All known taxa appear as rare, therefore their life cycles are poorly known, it is also problematic to decide, whether they are uni- or bivoltine. The data are usually scattered, and originated from different periods of the year, the majority of the specimens were collected in autumn, but *W. thailandica* was found in the late spring and in the summer. The early stages and the foodplants are unknown, the caterpillars presumably feed on trees and/or shrubs.

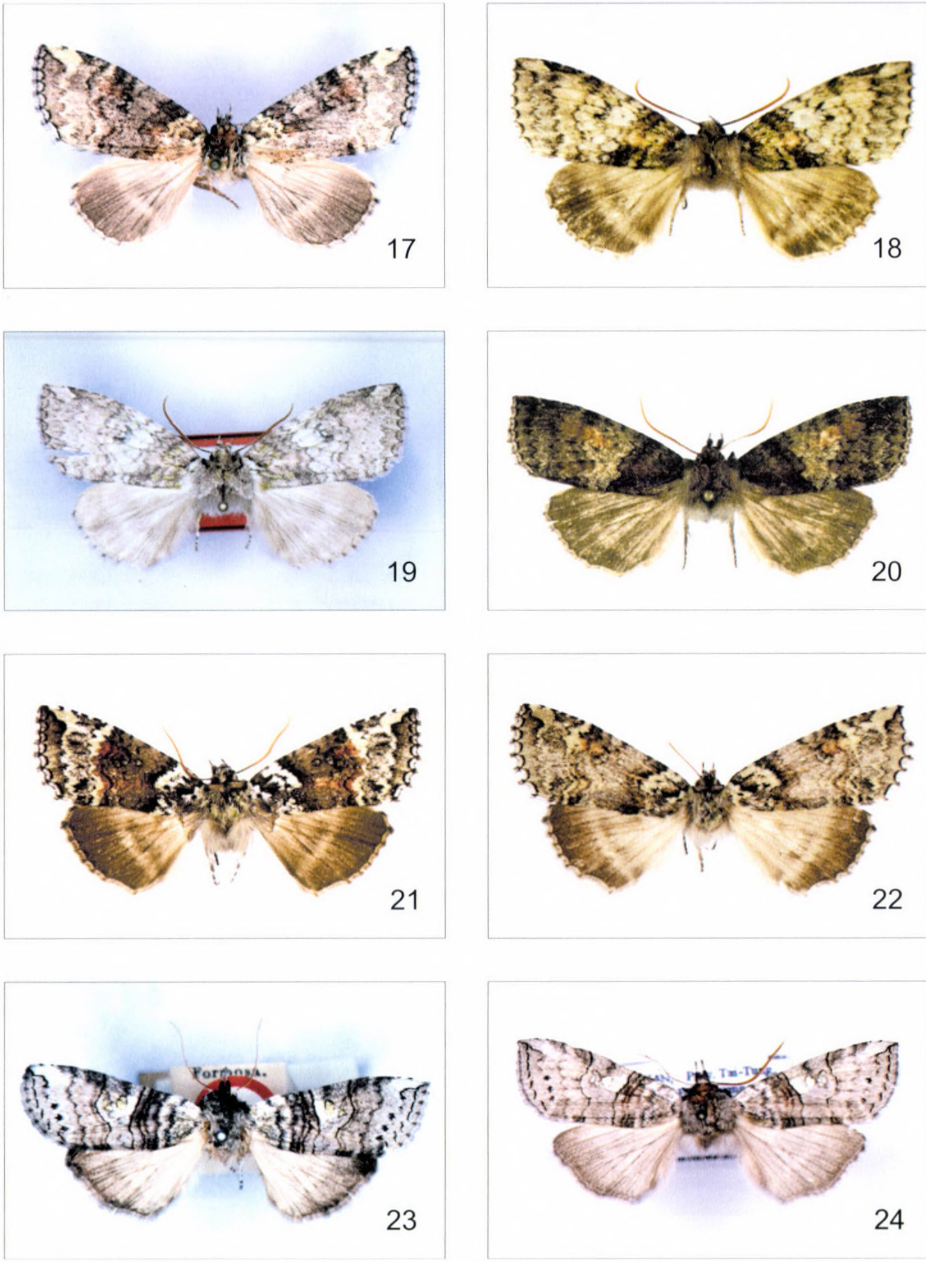
Distribution. A genus typical for the Himalayan region in wider sense, the majority of the species lives in the easternmost Himalayas in northern Indochina. The westernmost known locality is the Khasia Hills in Assam, there are two remote taxa in Taiwan and in the high mountainous plateau in Malaysia. The genus comprises different phyletic lines containing allopatric species, the taxa of the different lineages may occur sympatrically in Yünnan, N Thailand and N Vietnam.



Figs 1–8. 1–2 = *Wernya sechuana* sp. n.: 1 = holotype, male, 2 = paratype, female; 3–4 = *W. lineofracta* (HOULBERT, 1921): 3 = lectotype, male, 4 = paralectotype, male; 5–6 = *W. witti* sp. n.: 5 = holotype, male, 6 = paratype, female; 7 = *W. karsholti* sp. n., holotype, male; 8 = *W. rufifasciata* YOSHIMOTO, 1987, Taiwan, male



Figs 9–16. 9 = *Wernya rufifasciata* YOSHIMOTO, 1987, Taiwan, female; 10–11 = *W. thailandica thailandica* YOSHIMOTO, 1987, Thailand: 10 = male, 11 = female; 12–13 = *W. thailandica pallescens* ssp. n.: 12 = holotype, male, 13 = paratype, female; 14–15 = *W. solena* (SWINHOE, 1894): 14 = lectotype, male, 15 = India, Khasia Hills, male; 16 = *W. baenzigeri* YOSHIMOTO, 1995, holotype, male



Figs 17–24. 17 = *Wernya baenzigeri* YOSHIMOTO, 1995, paratype, female; 18–19 = *Wernya griseochrysa* sp. n.: 18 = holotype, male, 19 = paratype, male; 20 = *Chiropsestis rubrocinerea* sp. n., holotype, male; 21–22 = *Hiroshia albinigra* sp. n.: 21 = holotype, male, 22 = paratype, female; 23–24 = *Takapsestis (Takapsestis) wilemaniella wilemaniella* MATSUMURA, 1933, holotype of *Polyploca albibasis* WILEMAN, 1914: 23 = female, 24 = Taiwan, male



Figs 25–32. 25 = *Takapsestis (Takapsestis) wilemaniella wilemaniella* MATSUMURA, 1933, Taiwan, female; 26–27 = *T. (T.) w. continentalis* ssp. n.: 26 = holotype, female, 27 = paratype, male; 28–29 = *T. (T.) w. plumbeata* ssp. n.: 28 = holotype, female, 29 = paratype, male; 30–32 = *T. (T.) bifasciata* (HAMPSON, 1895): 30 = holotype, female, 31–32 = Nepal, male

Wernya sechuana sp. n.
(Figs 1–2, 49, 65)

Holotype. Male: "CHINA, SICHUAN, Daliang Shan, 1700 m, 30 km W of XIDE CITY, 19.8.-21.8.1997", gen. prep. No. RL6447 (W5156) (coll. Museum Witt).

Paratypes. 4 males, with the same data as the holotype (coll Museum Witt); 1 male, [China] Li-kiang, Prov. Nord-Yuennan, 2000 m, 2.10.1934, leg. H. Höne; 1 female, [China] Li-kiang, Prov. Nord-Yuennan, 2000 m, 1.10.1934, leg. H. Höne (coll. ZFMK).

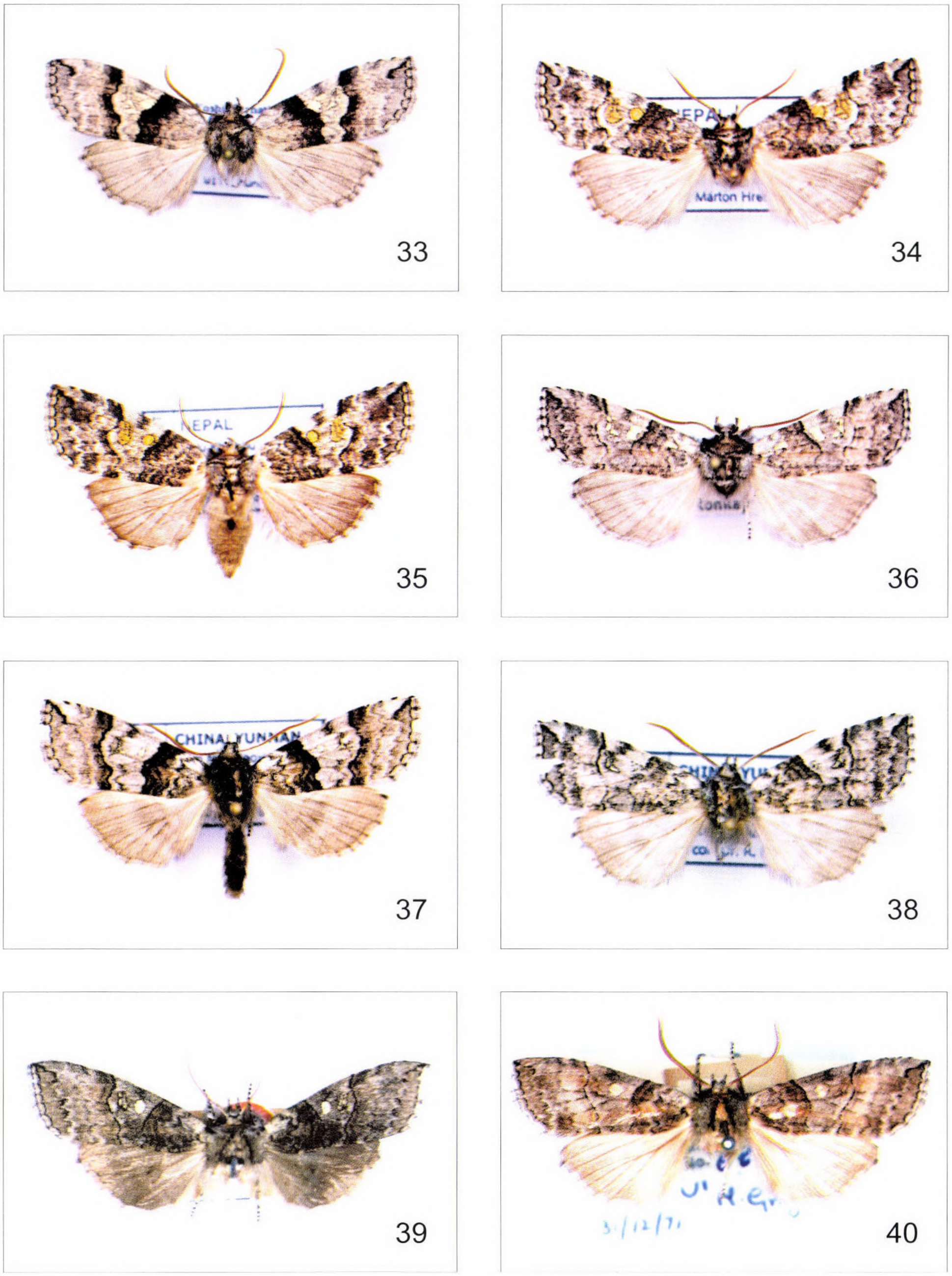
Gen. prep. Nos: males: LG963, LG965 (W5598), LG966 (W5599); female: LG964.

Diagnosis. The new species is very similar externally to *W. lineofracta* and *W. witti*, but the forewings are narrower with more pointed apex, the basal area is lighter, the praeterminal line (between the postmedial and subterminal lines) is less sinuous, less whitish and apically more angled, the subterminal line is also less sinuous, the hindwing and the underside of both wings are somewhat paler, with weaker dark fasciae. The fourth species of the group, *W. karsholti*, differs from *W. sechuana* by its longer forewings, more sharply defined antemedial, postmedial and praeterminal and less conspicuous, less whitish subterminal lines.

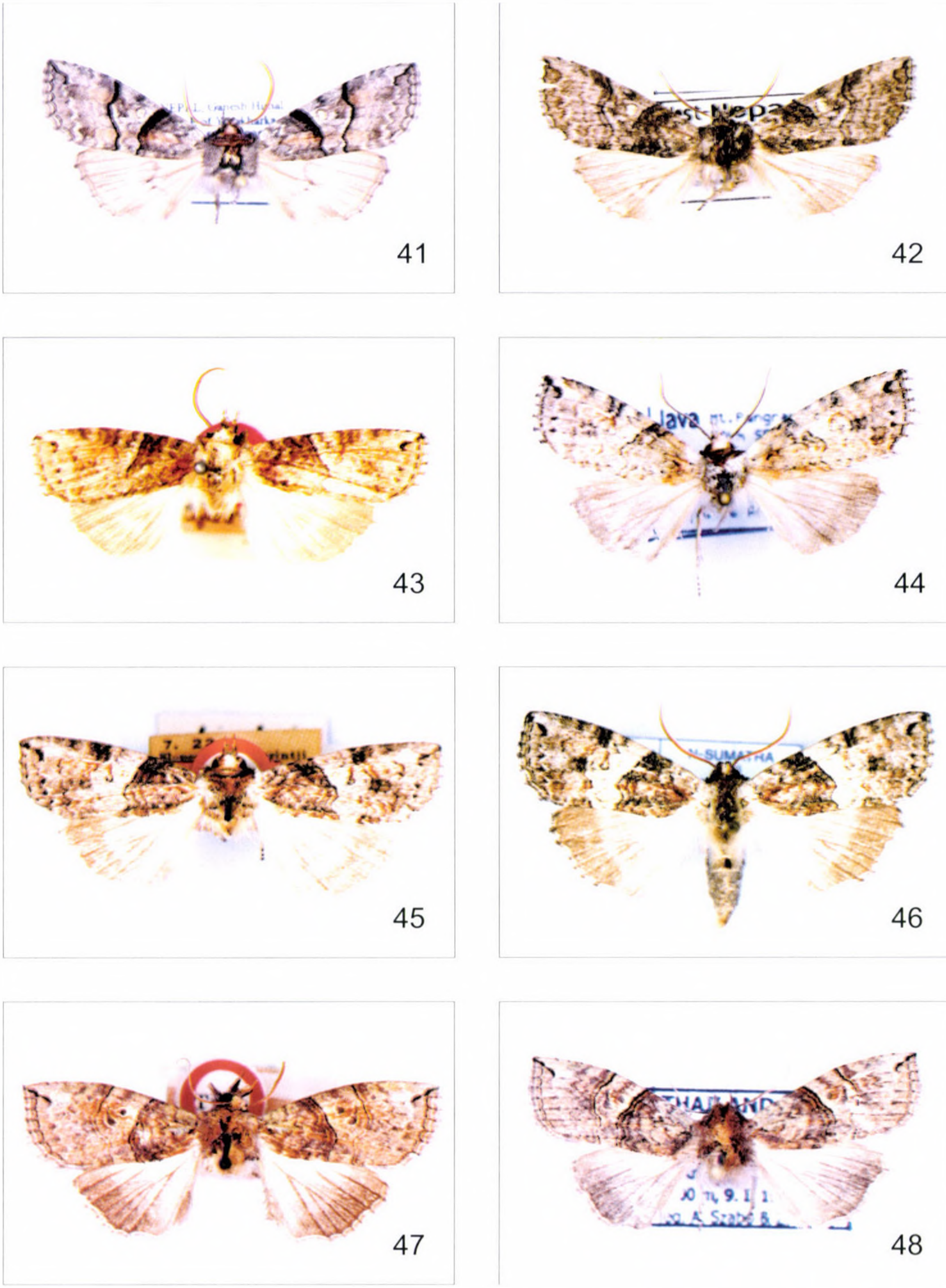
The male genitalia differ from those of *W. lineofracta* by its longer, apically more pointed arms of the uncus, much broader, triangular fultura superior with stronger dorsal dentition and by the broader, more rounded valva; from those of *W. witti* by their generally smaller size, longer, more pointed arms of the uncus, much weaker, smaller socii, broader but shorter, apically less dentated fultura superior, shorter aedeagus with more curved hook of the carina and with larger lateral, scobinate plates.

The female genitalia are very close to that of *W. witti* (the females of *W. lineofracta* and *W. karsholti* are unknown), but the ostial sclerotization is weaker, the ductus bursae is longer and the signum is smaller, shorter.

Description. Wingspan 40–47 mm, length of forewing 19–22 mm. Male. Head short, eyes large, frons broad, smooth, palpi porrect, slender, lateral sides dark brown, third joint relatively long, pale grey. Antenna brown, more or less filiform, laterally flattened, covered with very short cilia, with greyish scales on dorsal surface. Collar and thorax ashy grey, mixed with whitish, brown and dark grey hair-scales, metathoracic tuft rather big, brownish with blackish tip, metathorax with large, grey tufts of long hairs. Abdomen more brownish, covered with short hairs, dorsal crest absent. Forewing rather narrow, with pointed apex, outer margin finely crenulate. Ground colour dark ash-grey, basal area covered, marginal field irrorated with whitish-grey scales. Medial area darker, irrorated with dark brownish or fumous grey and pinkish orange scales. Subbasal, antemedial and postmedial crosslines double, sinuous, dark brownish grey, subbasal filled with whitish, ante- and postmedial with grey and pinkish scales. Basal line represented by short, blackish stripe and short dash, median fascia diffuse, shadow-like. Orbicular stigma a minute blackish dot, reniform fine, narrow, lunulate, blackish with small white spots. Praeterminal line simple, sinuous, dark grey, angled rather strongly near costa, defined by weak whitish grey inner shadow. Subterminal line distinct, sin-



Figs 33–40. 33–35 = *Takapsestis (Takapsestis) bifasciata* (HAMPSON, 1895): 33 = Nepal, male, 34–35 = Nepal, female; 36–38 = *T. (T.) fascinata* YOSHIMOTO, 1990: 36 = Vietnam, male, 37–38 = China, Yünnan, male; 39–40 = *T. (T.) orbicularis* (MOORE, 1888): 39 = lectotype, male, 40 = male, holotype of *Polyploca griseata* WARREN, 1915



Figs 41–48. 41–42 = *Takapsestis (Takapsestis) orbicularis* (MOORE, 1888), Nepal, male; 43–44 = *T. (Neogaurena) semiobsoleta semiobsoleta* (WARREN, 1915): holotype, male, 44 = Java, female; 45–46 = *T. (N.) s. sumatrensis* (GAEDE, 1930): 45 = holotype, male, 46 = paratype, male; 47–48 = *T. (Neotakatogaria) curvicosta* (WARREN, 1915): 47 = holotype, male, 48 = Thailand, female

uous, whitish grey, with large whitish apical patch, defined by strong but narrow, dark grey outer line. Terminal line black, consisting of fine black arches, cilia whitish grey with darker medial line, chequered with brownish at veins. Hindwing ochreous-whitish, suffused strongly with brownish grey, veins, broad, diffuse transverse line and marginal area darker. Discal spot rather indistinct, fine, arcuate, terminal line dark brown, cilia pale pinkish grey, spotted with darker brown. Underside of wings whitish grey, forewing with darker fumous grey suffusion, transverse lines broad, diffuse on both wings, discal spot of forewing absent, that of hindwing small, weak. Female. Similar to male, forewings somewhat broader.



Figs 49–52. Male genitalia apparatus of *Wernya* spp. 49 = *W. sechuana* sp. n., holotype; 50 = *W. lineofracta* (HOULBERT, 1921), lectotype; 51–52 = *W. witti* sp. n.: 51 = holotype; 52 = paratype

Male genitalia (Fig. 49). Uncus bifid with deep medial incision and rather narrow triangular, apically finely rounded arms. Tegumen broad, socii heavily sclerotized, apically chelate with hooked terminal processi, dorsal surfaces dentated, basal part with pyramidal protuberance. Fultura superior rather broad, triangular with arcuate margins, dorsal tip with small, finely dentate plate. Fultura inferior shield-like, sclerotized, with deep medial incision, ventral lobes small, trapezoidal, setose; vinculum short, strong, double-peaked. Valva rather short, broad, with apex finely rounded, with stronger, setose crests along sacculus. Sacculus short, narrow, scobinate, with weak medial crest. Aedeagus cylindrical, carina with strong ventral hook and high, scobinate lateral plates on both sides. Vesica short, tubular, upturned, weakly membranous, without cornuti.

Female genitalia (Fig. 65). Ovipositor short, papillae anales conical, finely scobinate and apically densely setose, apophyses short, slender. Sclerotized 8th segment forming a compact, broad ring, ventral plate with deep, V-shaped caudal incision; apophyses anteriores short, fine. Ostium bursae broadly V-shaped, less sclerotized, ductus bursae long, tubular, weakly membranous, corpus bursae ovoid, with a medium-long, narrow signum-stripe.

Bionomics and distribution. The short series of specimens were found at relatively low and medium altitudes in southern Sechuan and north Yünnan, at the end of August and at the beginning of October.

Etymology. The specific name refers to the home land of the new species.

Wernya lineofracta (HOULBERT, 1921) (Figs 3–4, 50)

Wernya lineofracta HOULBERT, 1921, In OBERTHÜR, *Études lépid. Comp.* **18**(2): 150, pl. 489, fig. 4002. Type-locality: [China], Ta-tsien-lou.

Type material examined. Syntype male, "Chasseurs Indigénes des Missionaires de Ta-tsien-Lou 1906; Cymatophora lineofracta Houlb.", "gen. prep. No.: RL6688"; syntype male, "Frontiére Orientale du Thibet, Chasseurs Indigénes du P. Dejean 1905", gen. prep. No.: BM.285. The first specimen is designated here as lectotype, the second is a paralectotype; both are in coll. BMNH.

Diagnosis. The external and genital differences between *W. lineofracta*, *W. sechuana*, *W. witti* and *W. karsholti* are discussed in the differential diagnoses of the related three species.

Description. Wingspan 44 mm, length of forewing 22 mm. Male. Pubescence of head and thorax dark brownish grey mixed with blackish, palpi dark grey, third joint pale grey; thoracic tufts large. Abdomen paler, greyish brown. Forewing broad, with pointed apex, outer margin finely crenulate. Ground colour shining silvery grey with intense dark brown-grey suffusion in medial area. Subbasal, antemedial and postmedial crosslines sharply defined, double, sinuous, dark brownish grey, filled with paler greyish, postmedial and praeterminal lines also with some rufous scales. Basal dash short, median fascia obsolete. Orbicular stigma hardly visible, a minute dot with whitish centre, reniform narrow, lunulate, blackish grey defined with small whitish grey spots. Praeterminal line double, sinuous, whitish grey and blackish, upper angle rather flat. Subterminal line rather distinct, strongly sinuous, whitish, with large apical patch and with dark grey-brown outer stripe. Terminal line sharply defined, consisting of fine black arches, cilia whitish grey, chequered with brownish.

Hindwing pale ochreous-whitish, suffused strongly with dark greyish brown, veins also brownish, broad, diffuse but relatively strong transverse line and marginal area even darker. Discal spot missing, terminal line dark brown, cilia whitish, spotted with darker brown. Female unknown.

Male genitalia (Fig. 50) Uncus, short, broad, bifid with relatively deep medial incision and rather broad, apically logged arms. Socii heavily sclerotized, apically chelate with hooked terminal processi, dorsal surfaces only slightly, basal part with slight protuberance. Fultura superior narrow, reversed T-shaped with more or less straight margins. Fultura inferior narrowly shield-like, sclerotized, with narrow, relatively deep medial incision; vinculum short, strong, double-peaked. Valva rather small, elongate, narrow, with finely rounded apex. Sacculus short, narrow, scobinate, with weak medial crest.

Bionomics and distribution. A poorly known species, known only by a pair of specimens from Ta-tsien-lou, no phaenological data are given.

Wernya witti sp. n.
(Figs 5–6, 51–53, 66)

Holotype. Male, "N VIETNAM, Mt. Fan-Si-Pan, N. Side, 1600 m, 22°17'N, 103°44'E, primary forest, 20-30.X.1995, leg. V. Sinjaev & E. Afonin", gen. prep. No.: RL6446 (W5157) (coll. Museum Witt).

Paratypes. 29 males, with the same data as the holotype; 1 male and 3 females, from the same locality, 1–7.XI.1995; 1 male, Mt. Fan-Si-Pan, W side, Cha Pa, secondary forest, 16–1800 m, 22°20'N, 103°40'E, 20–30.X.1994, SINJAEV & native collector leg.; 1 male, Mt. Fan-Si-Pan N side, Cha Pa, 2250 m, primary forest, 22°15'N, 103°45'E, 28–29.III.1995, SINJAEV & native collector leg.; 2 female, Mt. Fan-Si-Pan, N side, Cha Pa, 2250 m, primary forest, 22°17'N, 103°45'E, 28–29. III.1995, SINJAEV & native collector leg.; 17 males, 11 females, Mt. Fan-Si-Pan, N side, 2250 m, 22°17'N, 103°44'E, 1–6. XI.1995, leg. SINJAEV & AFONIN, ex coll. SCHINTLMEISTER; 1 female, Mt. Fan-Si-Pan (West), 1600–1800 m, Cha Pa, secondary forest, 22°20'N, 103°40'E, 20–30.X.1994 leg. SINJAEV & native collector; 19 males and 7 females, Mt. Fan-Si-Pan (West), 1600–1800 m, Cha Pa, secondary forest, 22°20'N, 103°40'E, XI.1994, leg. SINJAEV & native collector; 1 male, Tam Dao, 60 km NW Hanoi, 21°34'N, 105°20'E, 950 m, 17.X.1995, leg. SINJAEV (coll. Museum Witt and HNHM).

Gen. prep. Nos: males: RL6444 (W5158), RL6445 (W5161), RL6448 (W5159), RL6689; females RL6469 (W5160).

Diagnosis. The new species differs externally from the related *W. karsholti* by its broader forewings, weaker, less oblique antemedial, less sinuous, apically more straight praeterminal and by the more conspicuous, more sinuous, more whitish subterminal lines; the external differences between *W. sechuana* and *W. witti* are discussed in the diagnosis of *W. sechuana*.

The male genitalia differ from those of *W. lineofracta* and *W. sechuana* by its generally larger size and stronger sclerotization, broader but shorter arms of the uncus, much stronger socii, longer, reversed Y-shaped fultura superior with stronger dorsal dentition and by the larger valva; in addition, the aedeagus is longer, the

hook of the carina is weaker, less curved, and the lateral, scobinate plates are narrower, shorter than in *W. sechuana*.

Description. Wingspan 40–44 mm, length of forewing 20–22 mm. Male. Pubescence of head and collar brownish grey mixed with blackish and a few whitish hair-scales. Frons broad, smooth, sides of palpi dark grey, third joint pale grey. Antenna brown, scales on dorsal surface dark grey. Thorax dark ashy grey to fumous grey, mixed with whitish and brown hair-scales, metathoracic tuft large, brown with blackish tip, caudal end of metathorax with large tufts of long, pale grey hairs. Abdomen paler, greyish brown, covered with short hairs, dorsal crest absent. Forewing relatively broad, with apex pointed, outer margin finely crenulate. Ground colour dark grey with strong silvery shine and variably strong whitish and pinkish-rufous irroration. Subbasal, antemedial and postmedial crosslines rather sharply defined, double, sinuous, dark brownish grey, subbasal filled with whitish, ante- and postmedial with pinkish-rufous and grey scales. Basal line and dash short, blackish, median fascia obsolete. Orbicular stigma represented by minute blackish dot with whitish centre, reniform fine, narrow, lunulate, blackish grey with small whitish grey spots. Praeterminal line conspicuous, sinuous, white and dark grey, upper angle rather flat. Subterminal line sharply defined, sinuous, whitish, with large pale apical patch and narrow, dark grey outer line. Terminal line black, consisting of fine black arches, cilia whitish with darker medial line, chequered with brownish at veins. Hindwing pale ochreous, suffused strongly with dark greyish brown scales; veins, broad, diffuse but relatively strong transverse line and marginal area darkened. Discal spot indistinct or missing, terminal line dark brown, cilia whitish, spotted with darker brown. Underside of wings whitish grey, forewing with dark greyish brown suffusion, transverse lines broad, strong but diffuse on both wings. Marginal areas dark grey-brown, discal spot of forewing absent, that of hindwing small, rather strong. Female. As male, abdomen with huge, silvery greyish anal tuft.

Male genitalia (Figs 51–53). Uncus bifid with deep medial incision and rather broad, shortly triangular, apically rounded arms. Tegumen broad, socii heavily sclerotized, apically chelate with long, hooked terminal processi, dorsal surfaces strongly dentate, basal part with large cristate protuberance. Fultura superior reversed Y-shaped, dorsal tip with strong, dentate plate. Fultura inferior shield-like, sclerotized, with deep medial incision, ventral lobes small, trapezoidal, setose; vinculum short, strong, double-peaked. Valva rather long, broad, with apex finely pointed, with stronger, setose crests at base and along sacculus. Sacculus short, narrow, scobinate, with weak medial crest. Aedeagus cylindrical, carina with strong ventral hook and scobinate lateral plates on both sides. Vesica short, tubular, upturned, weakly membranous, without cornuti; medial part with small, dorso-lateral diverticulum.

Female genitalia (Fig. 66). Ovipositor short, papillae anales strong, conical, scobinate and setose, apophyses short, slender. 8th segment heavily sclerotized, forming a more or less compact, broad ring, ventral plate with deep caudal incision; apophyses short, fine. Ostium bursae V-shaped, narrow, ductus bursae long, tubular, weakly membranous, corpus bursae ovoid, with a long, cuneate signum.

Bionomics and distribution. The new species is known from two rather remote mountainous areas of North Vietnam (Fan-si-pan Mts and Tam Dao). The specimens were collected both in October–November and in March, it is still unclear whether the species is univoltine or it has two separated generations at the late autumn and in the early spring.

Etymology. The new species is named after Mr THOMAS WITT, a dedicated specialist of some "bombycoid" groups, the founder and owner of the Witt Museum, Munich.

Wernya karsholti sp. n.
(Figs 7, 54)

Holotype. Male, "Thailand, Chieng Mai, Doi Inthanon, 1600 m, 22–24.X.1984, Karsholt, Lomholdt and Nielsen leg.", gen. prep. No.: YOSHIMOTO HY1349 (coll. ZMC).

Diagnosis. The external differences between *W. lineofracta*, *W. sechuana*, *W. witti* and *W. karsholti* are discussed in the diagnoses of the preceding two species.

The male genitalia of the new species differ from those of *W. lineofracta*, *W. sechuana* and *W. witti* by its much narrower arms of uncus with considerably larger, deeper medial incision between them, weaker, narrower, trigonal fultura superior (the weakest, narrowest within the species-group); in addition, the aedeagus is shorter than that of *W. witti*, its ventral hook is the shortest compared with those of the related taxa.

Description. Wingspan 38 mm, length of forewing 14 mm. Male. Pubescence of head and collar brown–grey mixed with dark grey and whitish hair-scales. Sides of palpi dark grey-brown, third joint pale grey. Antenna brown, scales on dorsal surface greyish. Thorax ashy grey mixed with whitish and brown hair-scales, metathoracic tuft large, red-brown with blackish tip, metathorax with large tufts of long, grey hairs. Forewing relatively narrow, with apex pointed, outer margin finely crenulate. Ground colour ash-grey with strong silvery shine and whitish and pinkish-rufous irroration. Subbasal, antemedial and postmedial crosslines rather sharply defined, double, strongly sinuous, dark brownish grey, subbasal filled with whitish, ante- and postmedial with pinkish-rufous and grey scales. Basal line and dash short, blackish, median fascia obsolete. Antemedial line rather strong, oblique, orbicular stigma very small, dark grey circle with whitish centre, reniform fine, narrow, lunulate, blackish grey with small whitish grey spots and blackish dots at tips. Praeterminal line conspicuous, sinuous, white and dark grey, upper angle evenly arcuate. Subterminal line sinuous, whitish grey, with large whitish apical patch and conspicuous dark grey outer shadow. Terminal line sharply defined, consisting of fine black arches, cilia whitish with grey medial line, chequered with brownish at veins. Hindwing pale ochreous white, suffused with dark greyish brown, veins, transverse line and marginal area even darker brown. Discal spot poorly visible, terminal line dark brown, cilia whitish, spotted with darker brown.

Female unknown.

Male genitalia (Fig. 54). Uncus bifid with deep, broad medial incision, arms narrow, long, apically rounded. Tegumen broad, socii heavily sclerotized, apically chelate. Fultura superior narrow, trigonal, relatively weak, its dorsal tip with fine dentition. Fultura inferior shield-like, sclerotized, with deep medial incision, ventral lobes small, trapezoidal, setose; vinculum short, strong, double-peaked. Valva rather short, broad, with apex finely pointed, with stronger, setose crests at base and along sacculus. Sacculus short, narrow, scobinate, with weak medial crest. Aedeagus cylindrical, carina with strong but short, acute ventral hook and small, scobinate lateral plates.

Etymology. The new species is dedicated to Dr OLE KARSHOLT, specialist of several Microlepidopteran families, the collector of the unique specimen of the species.

Remarks. The species was published by YOSHIMOTO (1995) as *Wernya lineofracta.*

Wernya rufifasciata YOSHIMOTO, 1987
(Figs 8–9, 55, 67)

Wernya rufifasciata YOSHIMOTO, 1987, *Tyo Ga* **38**(1): 42. Type-locality: Formosa [Taiwan], Lantou Shien.

Type material examined. The black and white picture of the male holotype and the drawings of the male genitalia are published in the original description.

Additional material examined. 19 males and 8 females, from various localities from the mountainous areas of Taiwan, between 1700–2000 m altitudes.

Gen. prep. Nos: male: RL6450 (W5154); female: RL6470 (W5155).

Diagnosis. The species differs externally from the taxa of the *W. lineofracta* species group by its paler, more unicolorous brownish grey forewing ground colour and less intense dark covering of the medial field.

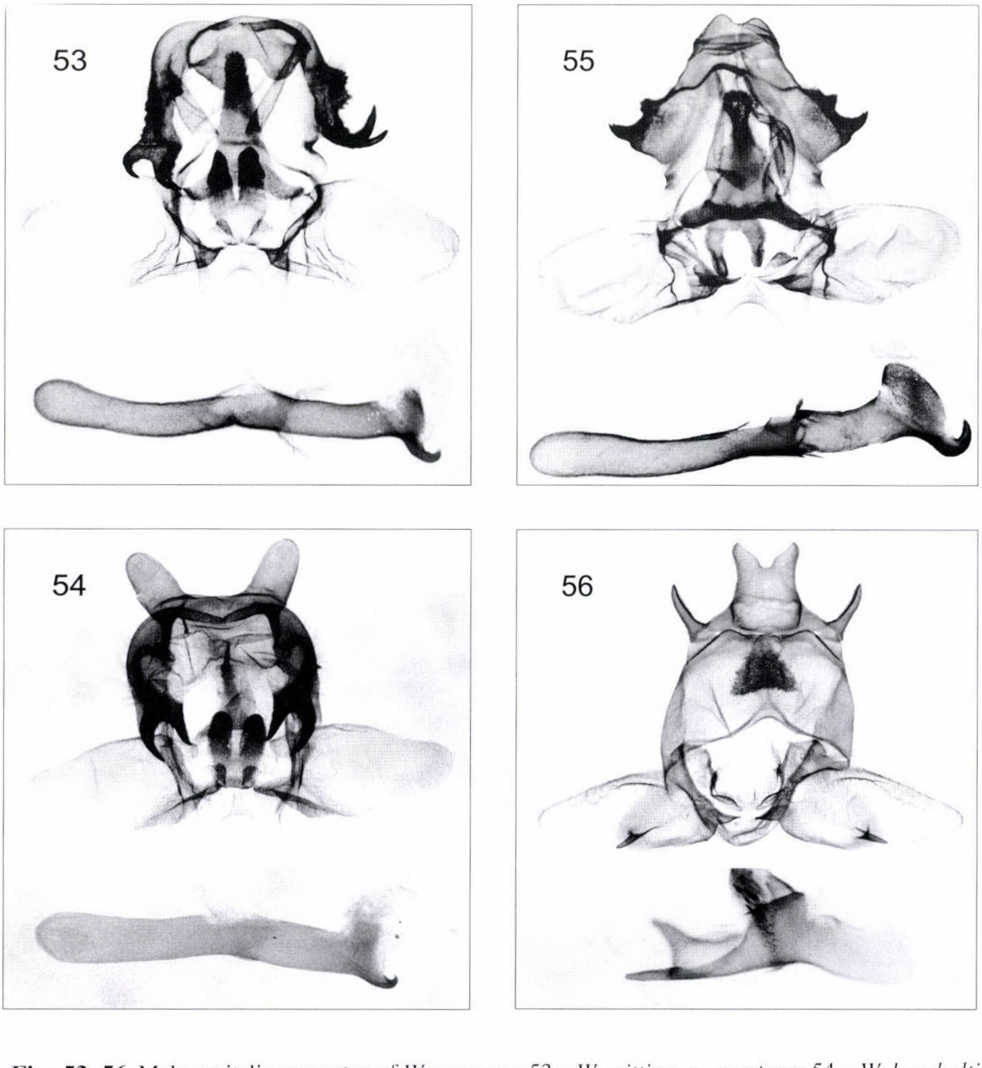
The male genitalia of *W. rufifasciata* differ from all the other members of the genus by its very broad tegumen with wide dorso-lateral lobes and double, triangular, apically dentate socii, the presence of a strong, apically rounded spinose process of fultura superior, the trapezoidal, apically only slightly incised uncus, the aedeagus is also conspicuously longer than those of the related taxa.

The unique features of the female genitalia of *W. rufifasciata* are the lack of the signum and the very strong, internally slightly dentate papillae anales.

Description. Wingspan 40–47 mm, length of forewing 20–23 mm. Male. Pubescence of head, collar and thorax brownish grey mixed with ochreous-whitish hair-scales; thoracic tufts well-developed. Forewing relatively broad, with apex pointed, outer margin finely crenulate. Ground colour dark, shiny brownish grey, irrorated with whitish and rufous scales. Crosslines rather sharply defined, double, usually sinuous, dark brownish grey, subbasal filled with whitish, ante- and postmedial with rufous and grey scales; median fascia obsolete. Orbicular stigma may be present as a small ring, reniform rather indistinct, lunulate or straight, blackish grey with small whitish grey spots. Praeterminal line more conspicuous, sinuous, defined with white scales, upper curve less arcuate. Subterminal line sharply defined, relatively broad, sinuous, whitish, defined with a few dark grey scales. Terminal line blackish, consisting of fine arches, cilia whitish, chequered with brown at veins. Hindwing pale ochreous, suffused strongly with darker brownish; veins somewhat darker, diffuse transverse line and marginal suffusion also darker greyish brown. Discal spot usually absent, cilia whitish, spotted with dark brown. Sexes similar, female has slightly broader forewing and huge greyish anal tuft.

Male genitalia (Fig. 55). Uncus very broad, more or less trapezoidal, slightly bifid with weak apical incision. Tegumen large, broad with wide dorso-lateral lobes, socii double, relatively small, sclerotized, more or less triangular, apically strongly dentate. Fultura superior broadly triangular with large, strongly spinose, terminally rounded apical process. Fultura inferior rather small, calyculate with deep, U-shaped medial incision; vinculum double-peaked. Valva broad, rounded, with strong transverse crest basally; sacculus short, relatively weak. Aedeagus cylindrical, very long, carina penis with strong ventral hook and large scobinate lateral plates on both sides, vesica short, upturned, with rather large, tubular medial diverticulum; cornuti absent.

Female genitalia (Fig. 67). Ovipositor short, robust, papillae anales strong, broadly conical, densely scobinate and setose; apophyses short, slender. 8th segment heavily sclerotized, dorsal and ventral plate more or less fused into compact, broad ring, ventral plate with deep, U-shaped caudal incision; apophyses short, fine. Ostium bursae U-shaped, ductus bursae long, tubular, twisted, weakly membranous with longitudinal wrinkles, corpus bursae elliptical, small, without signum. The female genitalia are described and illustrated here for the first time.



Figs 53–56. Male genitalia apparatus of *Wernya* spp. 53 = *W. witti* sp. n., paratype; 54 = *W. karsholti* sp. n., holotype; 55 = *W. rufifasciata* YOSHIMOTO, 1987, Taiwan; 56 = *W. thailandica thailandica* YOSHIMOTO, 1987, Thailand

Bionomics and distribution. The species is endemic to Taiwan, inhabiting the medium high and higher deciduous forest regions. Univoltine autumnal species, the imagines are on wing from the end of September to the beginning of November.

Remarks. Some of the type specimens, including the holotype, is labelled as "Formosa, Lantou, Shein 1969", which is probably a misunderstanding of Nantou Hsien (Nantou County).

Wernya thailandica thailandica YOSHIMOTO, 1987
(Figs 10–11, 56, 68)

Wernya thailandica YOSHIMOTO, 1987, *Tyo Ga* **38**(1): 46, figs 3, 4. Type-locality: Thailand, Chiang Mai.

Type material examined. The black and white pictures of the moths and the genitalia drawings of both sexes were published in the original description.

Additional material examined. A short series of both sexes from N Thailand (coll. BMNH and Museum Witt).

Gen. prep. Nos: male: LG1310 (W5621); female: LG1311 (W5622).

Diagnosis. The body of the species, similarly to the members of the *W. solena* group, is rather slender, differing from the larger, more robust taxa of the *W. lineofracta* and the *W. rufifasciata* groups. It is easily distinguishable from *W. solena* and *W. baenzigeri* by its more elongate forewings with less intense, more diffuse dark forewing markings, darker, not reddish-rufous irroration of the medial area and the stronger, darker reniform stigma.

The distinctive features of the male genitalia, compared with those of the other species of the genus, are the small fultura superior (the smallest within the genus), the quadrangular uncus with V-shaped apical incision, the presence of a fine, harpe-like valval process (*W. griseochrysa* has also a valval process, but it is much stronger, thicker), the well-developed, dentate vallum penis, and the double, acute, partly dentate extensions of the carina penis.

The female genitalia differ from those of the taxa of the *W. lineofracta* and *W. rufifasciata* groups by their separated dorsal and ventral plates of the 8th segment (those of the species of the latter groups form a continuous ring) and the shorter bursa copulatrix; from those of the *W. solena* group by the more acute, not divided papillae anales, the stronger, more quadrangular ostium bursae and the larger signum, and from those of *W. punctata* by the normal, not divided papillae anales.

The differences between the two subspecies of *W. t. thailandica* are discussed in the differential diagnosis of *W. t. pallescens*.

Description. Wingspan 33–43 mm, length of forewing 16–21 mm. Male. Pubescence of head and thorax whitish grey mixed with a few blackish, collar ochreous-brownish, its tip blackish. Frons broad, smooth, sides of palpi dark grey, third joint pale grey. Antenna fine, pale brown, with whitish scales on dorsal surface. Abdomen slightly paler than thorax, abdomen with huge, silvery greyish anal tuft. Forewing broad, with apex pointed, outer margin evenly arcuate. Ground colour whitish grey with strong silvery shine, medial and marginal areas irrorated usually strongly with darker brownish grey and reddish scales. Wing pattern rather diffuse, subbasal and antemedial crosslines forming wide, diffuse, oblique brownish fascia, basal line represented by small blackish spots. Orbicular stigma a small dot or missing, reniform narrow, lunulate or bar-like, both stigmata blackish grey. Postmedial and praeterminal lines less distinct, sinuous, brownish grey, with large blackish grey patches at costal margin. Subterminal line stronger, sinuous, whitish, with large, pale apical patch and narrow, diffuse, dark grey outer line. Terminal line fine, dark grey, continuous, cilia whitish, chequered with brownish at veins. Hindwing pale ochreous grey, transverse line diffuse, relatively strong, marginal area relatively narrow, dark brownish grey. Discal spot missing, terminal line dark brown, cilia white, spotted with brown. Underside of wings pale grey, basal part of forewing, transverse lines and marginal areas darker grey-brown. Female. Similar to male, but larger in size, forewing with somewhat stronger dark suffusion in medial area.

Male genitalia (Fig. 56). Uncus relatively narrow, quadratic with variably strong, V-shaped apical incision; socii short, simple, wedge-shaped. Fultura superior small, sclerotized, subtriangular or trapezoidal, covered densely with fine spiculi. Fultura inferior a narrow, fine, cup-shaped ribbon, vallum penis large, lobate, strongly dentate; vinculum very short, U-shaped. Valva small, relatively narrow, elongate with apex rounded or finely pointed. Ventral lamina of valva with stronger proximal sclerotized plate terminated in a harpe-like, rather long, often curved spine; sacculus short, less developed. Aedeagus short, cylindrical, angled at middle, carina penis with two strong ventral processi, left process usually broader, strongly serrate. Vesica short, recurved dorsally, membranous, without cornuti.

Female genitalia (Fig. 68). Ovipositor short, papillae anales strong, conical, scobinate and setose; apophyses short, slender. 8th segment sclerotized, ventral lamina separated into two stronger plates, dorsal lamina common, rather weak, without anterior incision; apophyses short, fine. Ostium bursae broad, sclerotized, more or less lyriform, ductus bursae short, weakly membranous, corpus bursae elliptical-ovoid, with small, elliptical signum.

Bionomics and distribution. The known area of the species is restricted to the northern mountains of Thailand, the specimens were found between 1000–1800 m a.s.l. It is hard to estimate whether it has a long, continuous brood or two, more or less overlapping generations, the few known examples were collected between May and September. The early stages and the larval foodplant are unknown.

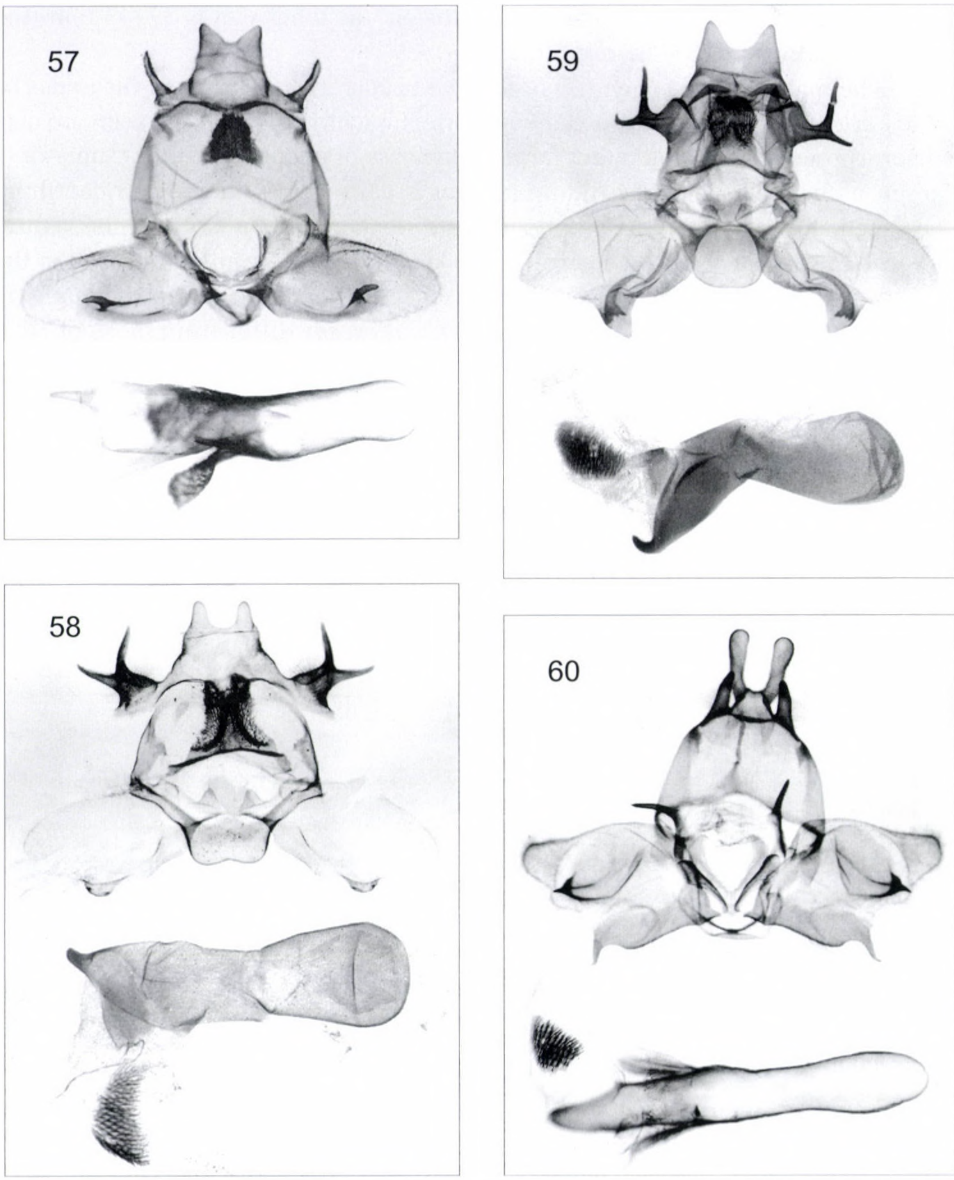
Wernya thailandica pallescens ssp. n.
(Figs 12–13, 57, 69)

Holotype. Male, "NORD-VIETNAM, Mt. Fan-si-pan, Cha pa, 2400 m, NN (22.15'N, 103.46'E), 8.-29.V.1993, leg. Sinajev & Simonov", gen. prep. No.: RL6515 (W5162) (coll. Museum Witt).

Paratypes. Vietnam. 2 females, 16–1800 m, Mt. Fan-Si-Pan (West), Cha Pa, secondary forest, (22°20'N, 103°40'E), 10.VI.–6.VII.1994, SCHINTLMEISTER leg.; 1 female, from the same locality,

30.VI.–12.VII.1994, BRECHLIN and SCHINTLMEISTER leg.; 1 male, from the same locality, IV.1995, SINJAEV & native collector leg. (coll. Museum Witt).

Gen. prep. No.: female: RL6471 (W5163)



Figs 57–60. Male genitalia apparatus of *Wernya* spp. 57 = *W. thailandica pallescens* ssp. n., holotype; 58 = *W. solena* (SWINHOE, 1894), lectotype; 59 = *W. baenzigeri* YOSHIMOTO, 1995, holotype; 60 = *W. griseochrysa* sp. n., holotype

Diagnosis. The new subspecies differs from *W. t. thailandica* by its generally paler medial part of the forewing with less diffuse crosslines, stronger orbicular and reniform stigmata, paler marginal area and paler hindwing with less conspicuous transverse line and dark marginal suffusion; the wingspan is 37–43 mm (the length of forewing is 18–21 mm).

The male genitalia (Fig. 57) of the two taxa are very close, but the uncus of *W. t. pallescens* is smaller, broader but shorter, apically tapering, the socii are narrower, shorter, originating rather far from the base of uncus, the fultura superior is larger, higher triangular, the fultura inferior is narrower, with stronger dentition, the saccular process ("harpe") is finer, more slender, and the arms of the ventral process of carina are different in size, the lateral, serrated arm is longer than the straight one while the ratio of these arms is just the opposite in *W. t. thailandica*.

The female genitalia (Fig. 69) of *W. t. pallescens* differ from those of *W. t. thailandica* by its stronger, broader ostium bursae, larger, more distinct ventral plates and weaker dorsal lamina of the 8th segment.

Bionomics and distribution. The species was found only in the northernmost part of Vietnam (Fan-Si-Pan Mts), the specimens were collected at the first half of the summer period (end of May to mid-July).

Etymology. The subspecific name refers to the pale greyish forewing ground colour of the species.

Wernya solena (SWINHOE, 1894)
(Figs 14–15, 58)

Gaurena solena SWINHOE, 1894, *Ann. Mag. nat. Hist.* **14**(6): 431. Type-locality: [India, Assam] Khasia Hills.

Type material examined. Male syntype, "Kahsia Hs. 94–66, Gaurena solena Swinhoe male type", gen. prep. No.: BM.30 (coll. BMNH); male syntype, "4338 male, Cherra Punji, Swinhoe coll., Gaurena solena male Swinhoe type", gen. prep. No.: BM.286 (coll BMNH); The first specimen is designated here as lectotype, the second is designated as paralectotype.

Additional material examined. Male, "Khasis Aug. 1896. Nat. coll., Gaurena solena male Swinhoe" (coll. BMNH).

Diagnosis. *W. solena* is an allopatric sister species of *W. baenzigeri*, the adults are often hardly separable from each other. *W. solena*, however, has paler forewing colouration with more intense whitish(ochreous) covering, especially in the marginal area, and the red-brownish irroration is more rosy-shaded in *W. baenzigeri*. The male genitalia show clearly recognizable differences, the most conspicuous is the shape of the socius, which is much broader, tricuspidate in *W.*

solena, without neck-like medial constriction, which is characteristic of the bicuspidate, much smaller socius of *W. baenzigeri*. In addition, the uncus of *W. solena* is significantly narrower with narrower, U-shaped incision, the dorsal part of the fultura superior is broader, less dentate, the vinculum and the saccular lobe are much smaller.

Description. Wingspan 36–37 mm. Male. Pubescence of head and thorax whitish grey mixed with brownish hair-scales, having often blackish tips, abdomen slightly paler greyish; antenna fine, pale brown, with whitish scales on dorsal surface. Forewing rather short, broad, with apex finely pointed, ground colour whitish-grey with fine ochreous sheen, medial area strongly irrorated with blackish grey and red-brownish scales. Basal and marginal areas wide, more or less clearly whitish, medial area narrow, antemedial and postmedial lines may join below cell. Subbasal, antemedial and postmedial lines double, sinuous, blackish grey filled with whitish or pale greyish scales, median fascia weak, indistinct. Praeterminal line usually less sinuous, simple, defined with whitish stripe, subterminal line strongly sinuous, whitish, defined mostly by its darker outer zone. Terminal line blackish, cilia white, spotted with blackish. Hindwing rounded, whitish, inner area weakly other parts strongly suffused with fuscous, marginal area broad, dark brown, veins and diffuse transverse line also brown. Cilia white, with brownish spots at veins. Female unknown.

Male genitalia (Fig. 58). Uncus bifid, more or less trapezoidal with deep, U-shaped medial incision and narrow, finely pointed arms. Tegumen high, broad, socii heavily sclerotized, flattened, tricuspidate with long, acute dorsal and medial and short ventral processi. Fultura superior sclerotized, large, subtriangular-trapezoidal, apically slightly incised and dentate; vinculum broad, strong, its ventral margin slightly depressed. Valva short, small, apically rounded, smooth, saccular part strongly sclerotized, with rounded distal lobe. Aedeagus short, cylindrical, carina penis with strong ventral hook and granulously sclerotized dorso-lateral plate. Vesica short, membranous, basally inflated, recurved dorsally, armed with a large cornuti field covered with short but strong spinules.

Bionomics and distribution. The species is known by three specimens from the Khasia Hills, Assam, N India, one of the specimens was collected in August. No additional data of its bionomy is available.

Remarks. The lectotype is labelled as "Kahsia Hs." which probably a misprinting of the Khasia Hills, the third specimen, collected two years later is already labelled as "Khasis".

Wernya baenzigeri YOSHIMOTO, 1996 **stat. n.**
(Figs 16–17, 59, 70)

Wernya solena baenzigeri YOSHIMOTO, 1996, *Tinea* **14**: 285, fig. 17. Type-locality: Thailand, Prov. Loei, Phu Luang.

Type material examined. Holotype male, "Thailand: Loei Province, Phu Luang Wildlife Sanctuary 8.–14.x.1984, 700–900 m, Karsholt, Lomholdt & Nielsen leg., Zool. Mus., Copenhagen", gen. prep. No.: HY-1348. Paratype female, "Thailand: Loei Province, Phu Luang Wildlife Sanctuary

10–12. x. 1984, 1400–1500 m, Karsholt, Lomholdt & Nielsen leg., Zool. Mus., Copenhagen", gen. prep. No.: HY-1350; both specimens are preserved in the collection of the ZMC.

Additional material examined. A short series of males from N Thailand.

Gen. prep. Nos: males: LG1307 (W5618), LG1308 (5619), LG1309 (5620), RL6687 (coll BMNH and Museum Witt).

Diagnosis. The comparison of *W. baenzigeri* with its twin species *W. solena* is given in the differential diagnosis of *W. solena*.

Description. Male. Head and thorax whitish grey mixed with brownish hair-scales, abdomen paler greyish. Forewing relatively short and broad, apically pointed. Ground colour shining whitish-grey, irrorated variably strongly with blackish grey and rosy-brownish scales. Basal and marginal areas wide, medial area narrow, antemedial and postmedial lines often joined below cell. Crosslines double, sinuous, blackish grey filled with pale whitish or greyish scales, median fascia hardly visible. Praeterminal line usually slightly waved, simple, defined with whitish inner stripe, subterminal line strongly sinuous, whitish, defined mostly by its darker outer line. Terminal line blackish, cilia white, chequered with blackish. Hindwing rounded, whitish, strongly suffused with brown; veins, transverse line and broad marginal area dark brown. Cilia white, with brownish spots at veins. Female. Similar to male, abdomen with large anal tuft.

Male genitalia (Fig. 59). Uncus trapezoidal with deep, broad medial incision and triangular, apically pointed arms. Tegumen high, broad, socii heavily sclerotized, bicuspidate with long, acute dorsal and medial processi and narrow medial "neck". Fultura superior sclerotized, large, subtriangular, apical part dilated, covered densely with short, strong spines; vinculum large, broad, strong, its ventral margin almost straight. Valva relatively short, apically rounded or slightly pointed, smooth, saccular part strongly sclerotized, with large, cristate, apically dentate distal lobe. Aedeagus short, cylindrical, carina penis with strong, bill-like, slightly hooked ventral process and large, sclerotized dorso-lateral plate. Vesica short, membranous, basally inflated, recurved dorsally, with a large cornuti field covered with short but strong spinules.

Female genitalia (Fig. 70). Ovipositor short, papillae anales divided into dorsal and ventral parts, ventral parts fused into stronger common plate, dorsal parts scobinate and setose; apophyses short, slender. 8th segment sclerotized, ventral plate with narrow medial incision; apophyses short, fine. Ostium bursae broadly calycular, weakly sclerotized, ductus bursae relatively short, weakly membranous, corpus bursae elliptical-ovoid, with narrow, medium-long signum.

Bionomics and distribution. The species was found in rather low and medium-high mountainous forests in northern Thailand, between 700–1700 m altitudes. The flight period is September–October.

Wernya punctata YOSHIMOTO, 1987

Wernya punctata YOSHIMOTO, 1987, *Tyo Ga* **38**(1): 47, figs 6, 16. Type-locality: Malaysia, [Cameron Highland], Tanah Rata.

Type material examined. The black and white pictures of the moth and the genitalia drawings of the holotype are given in the original description.

Diagnosis. The unique specimen of *W. punctata* is confusingly similar externally to the members of the *W. solena* and *W. thailandica* groups, the key feature mentioned in the original description (the presence of a strong orbicular spot) can also be found in some specimens of *W. thailandica*.

The female genitalia differ from those of the taxa of the *W. lineofracta* and *W. rufifasciata* groups by the divided papillae anales, the separated dorsal and ventral plates of the 8th segment and the shorter bursa copulatrix; from those of the *W. solena* group by the more acute, subtriangular ventral plate of the anal papillae. The distinctive features of *W. punctata* comparing with *W. thailandica* are the divided papillae anales and the longer, narrower signum.

Description. The external morphological characterization of the species is given following the original description of YOSHIMOTO. "Very similar to *W. solena* (SWINHOE) in appearance, but different from it in possession of orbicular on forewing. Head pale whitish gray; palpus dark brownish laterally, fringed below with brown hair; patagium pale whitish gray, its inner edge black, legs pale whitish gray, fore- and midtibiae ringed with blackish gray. Forewing pale whitish gray, with nearly the same maculation as in *W. solena*; antemedian area suffused with rufous below median nervure, outsidely limited by outer line of blackish antemedian line, which is minutely dentate above median nervure and excurved in cellule 2; orbicular small but conspicuous, ringed with blackish gray; reniform ill-defined, black, with whitish scales on it; postmedian area diffused with pale rufous, and defined outside by a serrate blackish line beyond postmedian line; a large grayish shade on subcosta; an apical streak angulated and leaving thin dents on veins 7 (R5) and 6 (M1); terminal line blackish, a series of thin lunules at end of cellules. Hindwing pale grayish ochreous, outer area darker. Underside: Forewing pale grayish ochreous, outer area dark; some black and white speckles on costa beyond middle. Hindwing pale grayish ochreous, outer one-fourth dark, with quite diffuse and obsolete median band. Lenght of forewing 22 mm (expanse 42 mm)."

Female genitalia. Ovipositor short, papillae anales strong, divided into two parts, ventral parts forming strong, ovoid plate, dorsal parts separated, narrow, setose. 8th segment sclerotized, ventral lamina producing two large, sclerotized trigonical lobes; apophyses anteriores short, fine. Ostium bursae weak, membranous, posterior part of ductus bursae swollen, finely sclerotized, corpus bursae elliptical-ovoid, with narrow, rather long signum.

Bionomics and distribution. The species is recorded only from the type locality where the unique type specimen was collected in autumn.

Wernya griseochrysa sp. n.
(Figs 18–19, 60–61)

Holotype. Male, "VIETNAM, Prov. Vinh Phu, Tam Dao, 1200 m, 105°39'24"E, 21°27'72"N, 11–13.XII.1997, leg. L. Peregovits and L. Ronkay", gen. prep. No.: RL6330 (coll. HNHM).

Paratype. Male, with the same data as the holotype (HNHM).

Gen. prep. No.: male: RL6503.

Diagnosis. The external appearance of *W. griseochrysa* is somewhat similar to those of *W. solena, W. rufifasciata* and the members of the *W. lineofracta*-line, but the new species is larger (wingspan 46–47 mm) with paler, shining silvery ash-grey forewing, the crosslines are more diffuse, the basal area with broad reddish zone along the antemedial line and with fine, but well-visible mossy green irroration at the inner half of the forewing, mostly at base and along veins.

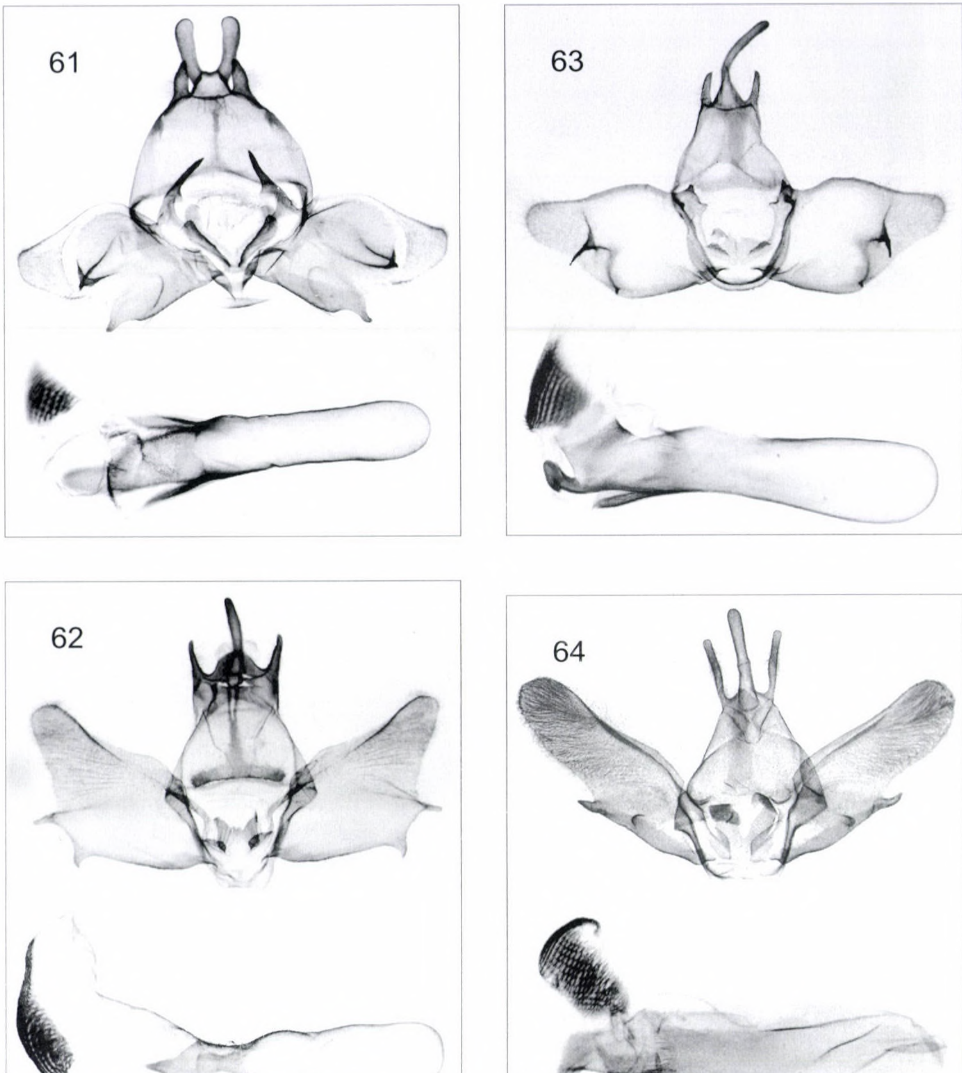
The male genitalia of *W. griseochrysa* differ from those of all known *Wernya* species by their bifid uncus consisting of long, slender arms, very short, thick but straight socii, long, thorn-like transtillar processi and by the large, sclerotized medial plate of the valva terminated in strong, wedge-shaped spine. The aedeagus is rather short, thick, the ventral plate of the carina is simple, long, beak-shaped.

Description. Wingspan 46–47 mm, length of forewing 22.5–23 mm. Male. Pubescence of head and thorax dark ashy grey mixed with violaceous brown and a few whitish hair-scales, vertex, collar and tegulae also with mossy green and blackish scales. Sides of palpi darker grey, third joint paler, antenna brown, scales on dorsal surface dark grey. Metathoracic tuft more brownish, caudal end of metathorax with long, paler grey hairs, abdomen also paler, greyish brown, covered with short hairs. Forewing relatively broad, with apex pointed, outer margin finely crenulate. Ground colour shining, dark ash-grey, basal area with mossy green, darker grey and pinkish-rufous irroration. Larger veins covered partly with greenish, inner half of marginal area suffused with pinkish scales. Basal line fine, blackish, subbasal, antemedial and postmedial crosslines double, sinuous, dark brownish grey, subbasal and antemedial lines and their pinkish-rufous filling form wide, oblique, darker zone. Median fascia fine, narrow, dark grey, postmedial line double, sinuous, dark grey, filled with pinkish scales. Orbicular stigma represented by a minute blackish dot with whitish centre, reniform lunulate, marked with blackish grey and whitish spots. Praeterminal line sinuous, rather diffuse, dark grey defined with pale grey, subterminal line also diffuse, sinuous, whitish, with large apical patch and narrow, dark grey outer line. Terminal line consisting of fine blackish arches, cilia pinkish-whitish with darker medial line, chequered with brownish at veins. Hindwing ochreous grey, transverse line and marginal area broad, diffuse, darker greyish brown. Discal spot small, indistinct or missing, terminal line dark brown, cilia pale brownish, spotted with darker brown. Underside of wings pale ochreous grey, inner area of forewing, diffuse transverse lines and marginal areas darker grey-brown, discal spots obsolete.

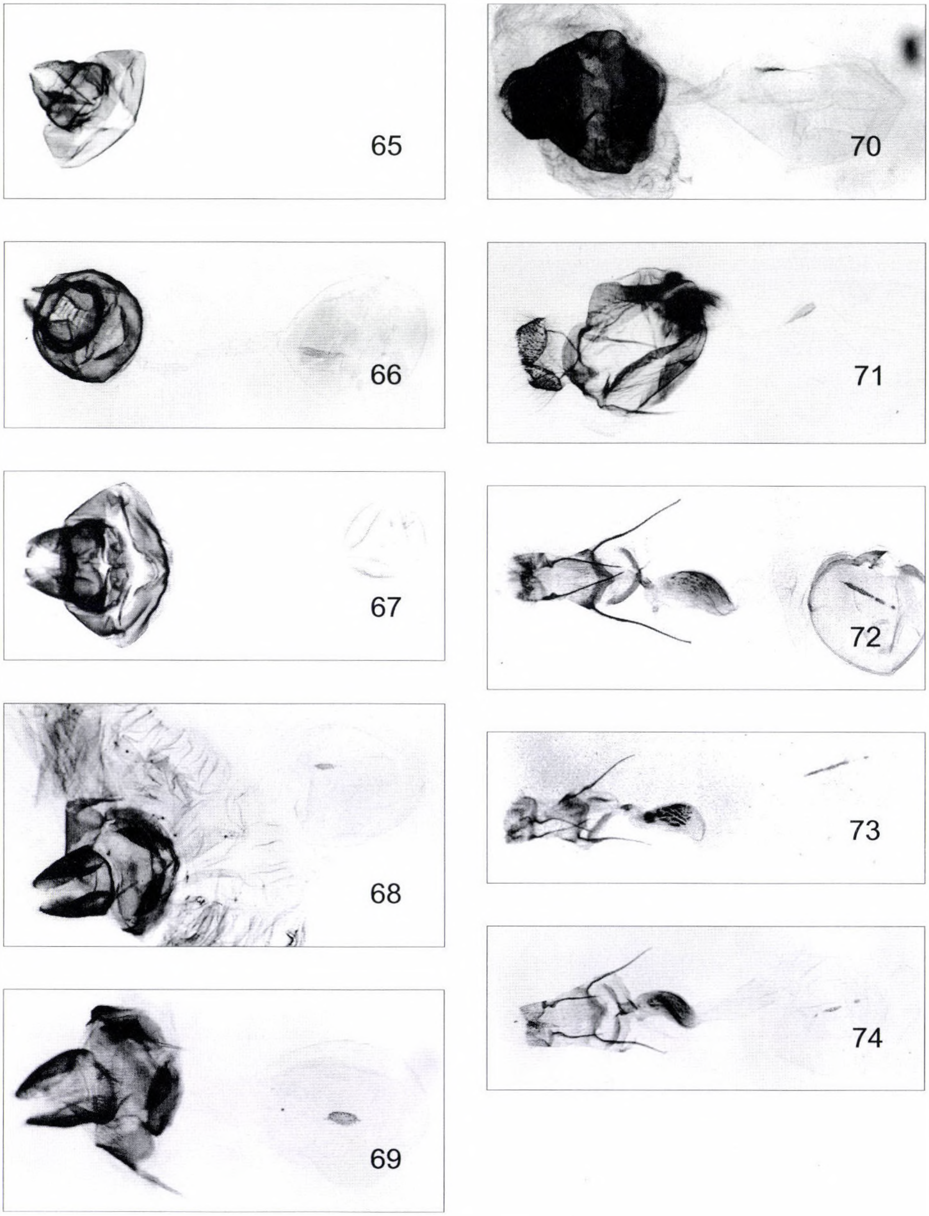
Male genitalia (Figs 60–61). Uncus bifid, U-shaped, its arms strong but slender; socii very short, simple, spine-like. Fultura superior represented by weak, narrow, sclerotized fascia, anellus membranous, covered densely with fine spiculi. Transtilla with large, curved dorso-lateral thorn, fultura inferior V-shaped, with stronger ventro-lateral bars; vinculum U-shaped. Valva broad, quadratic, with apex truncate triangular. Ventral lamina of valva with large medial sclerotized plate terminated in strong spine, sacculus sclerotized, long, narrow, with pointed apical extension. Aedeagus cylindrical, carina penis with long, beak-shaped ventral process, vesica with small cornuti field consisting of rather long, curved spines. Female unknown.

Bionomics and distribution. The two known specimens of the new species were collected at light along a mixed deciduous forest edge, the dominant trees of the forest are *Quercus*, *Castanea* and different Juglandaceae species. The two specimens were found at the same night, appearing rather early in the evening, interestingly, a day earlier, at a place being about 300 meters from this locality, a *Chiropsestis* species, *C. rubrocinerea* was collected at light.

Etymology. The specific name refers to the fine golden brilliance of the greyish forewings.



Figs 61–64. Male genitalia apparatus. 61 = *Wernya griseochrysa* sp. n., paratype; 62 = *Chiropsestis rubrocinerea* sp. n., holotype; 63 = *Hiroshia albinigra* sp. n., holotype; 64 = *Takapsestis (Takapsestis) wilemaniella wilemaniella* MATSUMURA, 1933, Taiwan



Figs 65–74. Female genitalia apparatus. 65 = *Wernya sechuana* sp. n., paratype; 66 = *W. witti* sp. n., paratype; 67 = *W. rufifasciata* YOSHIMOTO, 1987, Taiwan; 68 = *W. thailandica thailandica* YOSHIMOTO, 1987, Thailand; 69 = *W. thailandica pallescens* ssp. n., paratype; 70 = *W. baenzigeri* YOSHIMOTO, 1995, paratype; 71 = *Hiroshia albinigra* sp. n., paratype; 72 = *Takapsestis (Takapsestis) wilemaniella wilemaniella* MATSUMURA, 1933, Taiwan; 73 = *T. (T.) w. continentalis* ssp. n., holotype; 74 = *T. (T.) w. plumbeata* ssp. n., holotype

Chiropsestis gen. n.

Type-species: *Chiropsestis rubrocinerea* sp. n. Type-locality: Vietnam, Tam Dao.

Taxonomy. Monotypical genus; its phylogenetic relationships and the detailed comparison of the morphological features of most Polydactylini genera are discussed under the differential diagnosis of the genus *Wernya*.

Diagnosis. Large species (wingspan 50 mm), with long, rather narrow forewing with pointed apex, brownish ground colour with darker brown and rufous pattern, the species of this genus has the narrowest forewing within the genus-group. The differences between the genera of the tribe are given in the differential diagnosis of *Wernya*, the main distinctive genitalic characteristics are summarized below.

The male genitalia of *Chiropsestis* are easily distinguishable from those of *Wernya* by their slender, single uncus, short, straight, cuneate socii, broad, apically acute, quadrangular valvae with double saccular extensions (resembling slightly to those of *Takapsestis*) and by the long, inflated vesica armed with a huge field of strong, thick cornuti.

Comparing with those of *Hiroshia*, *Chiropsestis* has much larger, thicker aedeagus with beak-shaped, not hook-like process of carina, considerably broader tube of vesica with essentially larger field of strong cornuti and larger valva without sclerotized, acute processi, stronger sacculus with two terminal extensions. In addition, the uncus of *Chiropsestis* is shorter, with larger basal plate, the fultura superior is longer, the lobes of fultura inferior are larger, more setose and the vinculum is smaller, quadratic.

The main differences between the genitalia of *Chiropsestis* and *Mimopsestis* are as follows: the uncus of *Chiropsestis* is slender, straight, the socii are cuneate, not flattened-carinate, the fultura superior is reversed T-shaped with bifurcate dorsal end, the valva is more elongate without extension on the ventral surface and the saccular part is much broader with two pointed, flattened extensions terminally. The aedeagus is considerably shorter, broader, with beak-shaped ventral process of the carina, the vesica is much longer, broader, spacious, armed with long, strong cornuti arranged into a very large, elongate field.

Description. Head rather small, palpi long, slender, porrect, smoothly scaled. Frons smooth, with large tufts on vertex and at base of antennae. Thorax robust, pubescence rather homogeneous, collar and metathoracic tuft small, caudal end of metathorax with long hairs. Abdomen slender, dorsal crest absent. Forewing elongate, narrow, with apex pointed, outer margin finely crenulate. Wing pattern complete, although not very sharply defined, crosslines sinuous, basal dash reduced, median fascia obsolete. Hindwing also elongate, much shorter than forewing, almost unicolorous, base of wing and narrow submarginal fascia slightly paler, discal spot missing.

Male genitalia (Fig. 62). Uncus simple, slender, with rounded basal plate on ventral side, socii short, straight, fultura superior reversed T-shaped, with bifurcate dorsal part. Transtilla simple, without process, fultura inferior small, sclerotized, with small, rounded, densely setose lateral lobes, vinculum narrow, quadrangular. Valva broad, apically pointed, apical part wrinkled, finely hairy. Sacculus strong, broad, with two acute terminal extensions. Aedeagus strong, thick, carina with beak-like ventral process. Vesica rather long, broad, inflated, with huge field of strong, thick spines and denticles.

Female. Unknown.

Etymology. The new genus is named after the characteristic "chiropterous" shape of the male clasping apparatus, resembling an open-winged bat.

Chiropsestis rubrocinerea sp. n.
(Figs 20, 62)

Holotype. Male, "VIETNAM, Prov. Vinh Phu, Tam Dao, 1200 m, 105°39'24"E, 21°27'72"N, 11–13.XII.1997, leg. L. Peregovits and L. Ronkay", gen. prep. No. RL6329 (coll. HNHM).

Diagnosis. *C. rubrocinerea* resembles externally the *Wernya* species, especially to *W. rufifasciata*, but the forewings are longer, narrower, the rufous forewing markings are much more intense, the ground colour is darker grey, etc. The new species is also similar, because of its forewing shape, to the large *Tethea* OCHSENHEIMER, 1816 species of eastern-south-eastern Asia, but its body is more robust, the wings are broader, and the elements of pattern are rather different, more complex. The related *C. rubrocinerea* and *H. albinigra* are externally strongly dissimilar as *C. rubrocinerea* is narrow-winged, dark grey with rather diffuse darker grey and rufous pattern while *H. albinigra* is broad-winged, blackish-grey with more sharply defined silvery-whitish markings. In spite of this fact, their male genitalia are rather similar at first, although they differ in almost all details. The genital differences between *C. rubrocinerea* and the species of the related genera are discussed in detail in the diagnosis of the genus *Chiropsestis*.

Description. Wingspan 50 mm, length of forewing 24 mm. Male. Head and thorax dark plumbeous grey, vertex, collar and edges of tegulae mixed with orange-brown hair-scales. Palpi dark grey, antenna brown, scales on dorsal surface greyish. Metathoracic tuft small, dark grey-brown with darker tip, caudal end of metathorax with long grey hairs. Abdomen somewhat paler, more brownish, dorsal crest absent. Forewing elongate, narrow, with apex pointed, outer margin finely crenulate. Ground colour dark, shining plumbeous grey, broad basal area, outer part of cell, and two long fascia along cubital and anal veins irrorated with orange-brown, narrow medial area with whitish grey scales. Crosslines rather indistinct, sinuous, dark grey or grey-brown or partly orange-brown. Subbasal, medial, postmedial and praeterminal lines diffuse, antemedial and subterminal lines rather sharply defined. Basal line and dash reduced, median fascia obsolete. Orbicular stigma very small, rounded, red-brown, reniform rather indistinct, elliptical, incompletely encircled with fine red-brownish

line, filled with pale orange-brown, lower part with small dark grey spot. Praeterminal line obsolescent, diffuse, sinuous, dark grey, subterminal line also sinuous, whitish grey, its dark grey outer fascia somewhat darker, stronger than praeterminal line. Terminal line more or less continuous, consisting of a row of dark grey arches, cilia dark greyish, spotted with whitish. Hindwing almost uniformly dark grey-brown, base of wing and narrow fascia between transverse stripe and marginal area slightly paler. Discal spot missing, terminal line dark brown, cilia greyish brown. Underside of wings grey, inner area of forewing, transverse lines and marginal areas suffused with darker brownish grey scales.

Male genitalia (Fig. 62). They are characterized in the diagnosis of the new genus.

Bionomics and distribution. The new species is known by its holotype, from the type locality only. The brief characterization of the collecting site is given under the bionomics of its sympatric and syntopic relative, *Wernya griseochrysa*.

Etymology. The specific name refers to the colouration of the forewing of the new species.

Hiroshia gen. n.

Type-species: *Hiroshia albinigra* sp. n. Type-locality: N Vietnam, Fan-si-pan Mts.

Taxonomy. Monotypical genus; its phylogenetic relationships and the detailed comparison of the morphological features of most Polydactylini genera are discussed under the differential diagnosis of the genus *Wernya*.

Diagnosis. The external appearance of the single known species of the genus is similar to that of the taxa of the genus *Wernya*, but the ground colour is darker, deep chocolate-brown, and a part of the wing pattern is clear white. Another important distinctive feature is the lack of the huge anal tuft of the female in case of *Hiroshia*. The species of the other similar genus, *Chiropsestis*, has narrower, longer forewings with brownish ground colour, but without whitish pattern.

The male genitalia differ from those of *Wernya* by its simple uncus, short, acute socii, apically more elongate valva with less sclerotized, almost membranous basal part and with large, acute medial and fine, short ventral extensions, flattened hook of carina with its tip directed ventro-laterally; from those of *Chiropsestis* by the much shorter, narrower vesica with essentially smaller, weaker field of cornuti, the hooked, not beak-shaped ventral process of the carina, the different shape of valva with more elongate cucullus, the presence of the acute valval extensions and the lack of the double saccular processi and the absence of the basal plate of the uncus; from those of *Mimopsestis* by its slender, straight uncus and socii, reversed T-shaped, not bilobate fultura superior, distally tapering valva with two acute, not lobate or crest-like extensions, much shorter, thicker aedeagus with hooked carina

and the significantly longer, broader vesica with the cornuti field consisting of separate, chevron-like cornuti.

The female genitalia of *Hiroshia* and *Wernya* are rather dissimilar as the ostial part of *Hiroshia* is huge, sclerotized, the ductus bursae is short, and the distal third of the corpus bursae has scobinate, slight folds and a stronger ventro-lateral crest, while the known females of *Wernya* have considerably smaller, trapezoidal or cup-shaped ostial part and the distal third of the corpus bursae is membranous.

The size and the shape of the ostial part is similar in *Hiroshia* and *Mimopsestis*, but the sclerotization of this region is weaker in *Hiroshia*, the ductus bursae is stronger, crest-like in *Mimopsestis*, but the distal half of the corpus bursae is long, tubular, membranous. In addition, the papillae anales of *Hiroshia* are membranous, simple, without sclerotized plate between them on the ventral side, while the papillae of *Mimopsestis* are sclerotized, double, with a trigonal sclerotized ventral plate between them.

Description. Large, broad-winged species (wingspan 46–51 mm), with strong body, well-developed thoracis tufts, anal tuft of female absent. The more detailed external characterization is given in the description of the type species.

Male genitalia (Fig. 63). Uncus simple, slender, long, with triangular basal plate, socii short, straight, fultura superior reversed T-shaped. Transtilla with double-peaked lobe at base of valva, fultura inferior small, sclerotized, quadrangular, lateral lobes small, elongated, cristate, vinculum broad, arcuate. Valva broad, apically pointed, with a large, strong, acute subcostal and a small, spine-like ventral processes along distal edge of sacculus. Aedeagus strong, thick, carina with strong, flattened ventral hook curved laterally, its tip directed ventro-laterally. Vesica upturned, inflated tube, with large field of strong cornuti continuing in fine stripe of short, weak spiculi extending towards ductus ejaculatorius.

Female genitalia (Fig. 71). Ovipositor short, papillae anales membranous, broad, densely setose, without sclerotized plate, penultimate segment forming narrow sclerotized half-ring dorsally. Ostial part huge, granulosely sclerotized, more or less U-shaped, ductus bursae very short, flattened, appendix bursae situated very close to gonoporus. Distal end of corpus bursae flattened, with scobinate, slight folds and a stronger ventro-lateral crest, medial part membranous, wrinkled, proximal part discoidal, membranous with fine wrinkles, signum rather large, lanceolate, dentate.

Etymology. The new genus is named after Dr HIROSHI YOSHIMOTO, expert of the family Thyatiridae.

Hiroshia albinigra sp. n.
(Figs 21–22, 63, 71)

Holotype. Male, "N-VIETNAM/Tonkin, Mt. Fan-Si-Pan (Nord), Cha Pa, Nebelwald, (22°15'N, 103°45'E), 2–4.3.1995, 2240 m, leg. Dr. R. Brechlin", gen. prep. No.: RL6472 (W5164) (coll. Museum Witt).

Paratypes. 1 male, with the same data as the holotype; 4 males, 2 female, N Vietnam, Mt. Fan-si-pan, N Side, Cha Pa, 1600 m, 22°17'N, 103°44'E, primary forest, 20–30.IV.1995, leg. SINJAEV & native collector; 1 males and 1 female, same locality, 15–25.IV.1995, leg. SINJAEV & native collector; 4 males, Mt. Fan-si-pan, Cha Pa, 22°17'N, 103°44'E, 25–30.III.1995, 1600 m, leg. SINJAEV & SCHINTLMEISTER; 2 males, Mt. Fan-si-pan, Cha Pa, 22°15'N, 103°45'E, 2250 m, 28–29.III.1995, leg SINJAEV (coll. Museum Witt and HNHM).

Gen. prep. Nos: males: RL6449 (W5166), RL6514 (W5165); female: RL6513 (W5167).

Diagnosis. *Hiroshia albinigra* differs from the taxa of the genus *Wernya* by its significantly darker colouration of both wings, the blackish grey forewing ground colour and the strong, rather broad, diffuse, clear white antemedial, praeterminal and subterminal crosslines, and by the conspicuously different genitalia of both sexes.

The differences between *H. albinigra* and *Chiropsestis rubrocinerea* are discussed in detail under the diagnosis of the latter species.

Description. Wingspan 46–51 mm, length of forewing 22–25 mm. Male. Head blackish, marked with white, collar brownish with black apical stripe. Antenna brown, with grey scales on dorsal surface. Tegulae greenish white with blackish hair-scales, metathoracic tuft with blackish tip, caudal end of metathorax with long brownish grey hairs. Forewing relatively broad, with pointed apex, outer margin finely crenulate. Ground colour dark chocolate-brown with violaceous shine, basal and marginal areas with variably strong white suffusion and reddish-rosy irroration. Subbasal, antemedial and postmedial crosslines rather indistinct, double, sinuous, blackish grey, subbasal filled with whitish, antemedial with blackish grey, postmedial partly with deep red-brown scales. Basal line and dash short, strong, black, median fascia weak, shadow-like. Orbicular stigma represented by small blackish ring with whitish centre, reniform relatively large, bean-shaped, with fine black outline, its filling partly pale greyish. Praeterminal line appears as conspicuous, sinuous white fascia with interrupted, black outer line. Subterminal line rather diffuse, sinuous, white, defined with black streaks and spots on veins. Terminal line strong, consisting of fine black arches, cilia silvery whitish with darker medial line, chequered with blackish grey at veins. Hindwing pale ochreous, suffused strongly with dark brown, veins, transverse line and broad marginal area even darker. Discal spot missing or shadow-like, terminal line dark brown, inner half of cilia brown, outer part whitish. Underside of wings pale ochreous grey, forewing with dark brownish grey suffusion, transverse lines broad, strong but diffuse on both wings. Marginal areas dark grey, discal spot of hindwing diffuse. Female. Similar to male but larger in size, forewings somewhat broader, ground colour paler, more greyish with less intense reddish irroration; abdomen without large anal tuft.

The descriptions of the genitalia are given in the description of the genus.

Bionomics and distribution. The new species is only known from the higher forest zones of the Fan-si-pan, the adults are on wing in the spring period (March–April).

Etymology. The specific name refers to the dark (blackish) forewing ground colour and the contrasting white crosslines of the new species.

2. THE GENUS *TAKAPSESTIS* S. L.

Takapsestis MATSUMURA, 1933

Takapsestis MATSUMURA, 1933, *Insecta Matsumurana* 7: 200. Type-species: *Takapsestis wilemaniella* MATSUMURA, 1933. Type-locality: [Taiwan] Formosa.

History. The genus was erected by MATSUMURA in 1933 for a single species, *Takapsestis wilemaniella* MATSUMURA, 1933 (= *Polyploca albibasis* WILEMAN, 1914, nom. praeocc.), and has long been considered as a monotypic unit, being endemic to Taiwan.

The genus is mentioned by FORBES (1936) as one of the genera described by MATSUMURA based largely on points of venation. As he had no opportunity to study specimens of *Takapsestis*, the genus is missing from his comprehensive analysis of the known Thyatirine genera.

The unfortunately incomplete monographic work of WERNY (1966) covers the revisions of the tribes Thyatirini, Macrothyatirini, Habrosynini and Tetheini, the genus *Takapsestis* is absent also from the sketch of the generic content of the other six tribes (op. cit.: 7–9).

Subsequently, YOSHIMOTO had published a series of papers dealing with the taxonomy and biogeography of the subfamily Thyatirinae, four of them (1983, 1990, 1992, 1994) containing statements, illustrations and data concerning this genus. As a result of the revision of numerous eastern and south-eastern Asian thyatirine species, four taxa were transferred by him into *Takapsestis* (1983). The next item of this series dealing with the genus (1990) can be considered as the first taxonomic survey of *Takapsestis* (although it was not titled as a revision of the genus), with the description of a new species and the transfer of further two species into *Takapsestis*. Finally he described two additional species from Nepal in the Moths of Nepal series (1992, 1994); but no further taxonomic analysis of the genus was published by him.

The Sumatran species of the genus is discussed and illustrated by KOBES (1985); additional notes on the taxonomy of the genus are given by HOLLOWAY (1998).

Taxonomy. The genus is rather problematic from taxonomic point of view. One of the main reasons is that most species of the genus are known only by a few specimens although *T. wilemaniella* and *T. bifasciata* are represented in larger series in certain collections. The majority of the species, according to the results of the intense faunistic exploration of large areas of eastern and south-eastern Asia, proved to be rare, known only from very few, strongly scattered localities being

rather remote from each other. Moreover, most taxa are highly variable in size and colouration, sometimes also in the wing shape; in addition, the genital configuration of the externally often strongly different species is surprisingly similar, the differences between the taxa of the three subgenera are also small.

In our concept, *Takapsestis* contains three phyletic lineages, which are considered as subgenera, *Takapsestis* s. str., *Neogaurena* ROEPKE, 1944, **stat. rev.** and *Neotakatogaria* **subg. n.** (for *T. curvicosta* (WARREN, 1915), resp.

Synopsis

Takapsestis MATSUMURA, 1933

Subgenus *Takapsestis* MATSUMURA, 1933, *Insecta matsumurana* **7**: 200. Type-species: *Takapsestis wilemaniella* MATSUMURA, 1933. Type-locality: [Taiwan] Formosa, [Puli] Horisha.

wilemaniella wilemaniella MATSUMURA, 1933. Type-locality: [Taiwan] Formosa, [Puli] Horisha.
albibasis WILEMAN, 1914. Type-locality: [Taiwan] Formosa, [Alishan Mt.] Arizan.
wilemaniella continentalis **ssp. n.** Type-locality: Vietnam, Fan-si-pan.
wilemaniella plumbeata **ssp. n.** Type-locality: Nepal, Solu Khumbu.
bifasciata (HAMPSON, 1895). Type-locality: India, Darjeeling.
nepalensis YOSHIMOTO, 1992. Type-locality: Nepal, Godavari; **syn. n.**
harutai YOSHIMOTO, 1994. Type-locality: Nepal, Koshi; **syn. n.**
fascinata YOSHIMOTO, 1990. Type-locality: China, Yünnan, A-tun-tse.
orbicularis (MOORE, 1888). Type-locality: India, Kangra district, Dharmsala.
griseata (WARREN, 1915). Type-locality: India, Kangra district; **syn. n.**

Subgenus *Neogaurena* ROEPKE, 1944, **stat. n.**, *Natuurhistorisch Maandblad* **33**: 65. *Type-species: Neogaurena grisescens* ROEPKE, 1944. Type-locality: Java, Potachawattee.

semiobsoleta semiobsoleta (WARREN, 1915). Type-locality: Java, Pengalengan.
grisescens (ROEPKE, 1944). Type-locality: Java, Potachawattee.
semiobsoleta sumatrensis (GAEDE, 1930). Type-locality: Sumatra, Khorintji Mt.; **stat. n.**

Subgenus *Neotakatogaria* **subg. n.** Type-species: *Polyploca curvicosta* WARREN, 1915. Type-locality: India, Khasis.

curvicosta (WARREN, 1915). Type-locality: India, Khasis.

Diagnosis. The genus belongs to the tribe Demopsestini, its closest relatives are *Neoploca* and *Epipsestis*. The species of *Takapsestis* resemble externally, besides the taxa of the two genera mentioned above, to the members of the genera *Demopsestis*, *Asphalia*, *Achlya* and *Polyploca*; even the wing venation of these genera is also rather similar, except in the case of *Asphalia*. Although the species of these genera may differ in the length and density of the hairs of the eyes, the wing shape and the strength of the body, the more remarkable differences can be found in the configuration of the genitalia.

The ground plan of the male genitalia are also similar in the genera *Takapsestis, Neoploca, Epipsestis, Demopsestis* and *Asphalia*, while those of *Achlya* and *Polyploca* are strongly different by their quite dissimilar uncus-socius complex. In *Takapsestis* the sacculus has two, more or less sclerotized processi at the middle and at distal end of the ventral margin; the sacculi of *Neoploca, Epipsestis* and *Asphalia* have only a single, acute, lobate or folded, often dentate or setose extension, while *Demopsestis* has two processi, but they are much enlarged and the saccular sclerotization is much stronger than in the other genera. The uncus and the socii of the above-mentioned genera are simple, stick- or bar-like, except in *Epipsestis*, where the socii are regularly flattened, folded, sometimes lobate or even furcate or double and the uncus may be enlarged, flattened or bifurcate. The tegumen of *Takapsestis* is longer, narrower than those the related genera (this is the distinctive feature between *Takapsestis* and *Neoploca*); the fultura superior is weak, narrow, that of *Epipsestis* is always well-developed, covered (at least partly) with teeth. The carina of aedeagus is a strong ventral hook in *Takapsestis* and *Neoploca*, a short hook in *Asphalia*, a flattened, often twisted plate in *Demopsestis* and *Epipsestis*; the vesica of these genera are similar in type, short, membranous, recurved, with a variable large cornuti field.

The female genitalia of *Takapsestis* differ from those of *Epipsestis*, *Demopsestis* and *Asphalia* by the presence of the swollen, verrucose and wrinkled posterior (or medial) sector of the tubular distal part of bursa and the most often different shape of signum (which may be absent in *Epipsestis*). This swollen part is present in *Neoploca*, but the signum is characteristically rounded, not bar- or ribbon-like and the antevaginal plates are patch-like.

The species of *Takapsestis* may be also similar to certain species of *Neotogaria*, but the second segment of palpi of the *Neotogaria* species are consid-

erably broadened, thicker, the third segment is much shorter and the eyes are naked, being significantly larger than those of *Takapsestis*.

The male genitalia of the genera *Neotogaria* (and *Chaeopsestis*) are also similar to those of *Takapsestis* and its close relatives, but have less sclerotized sacculus, without the two ventral processi, being characteristic to *Takapsestis*, only a small, pointed lobe (*Neotogaria anguligera*) or a few small dentate folds (*Chaeopsestis*) may be present; the uncus of *Neotogaria* is more than twice as long as the socii; the carina is most often simple, the vesica is considerably longer, without cornuti.

The female genitalia of *Neotogaria* and *Chaeopsestis* differ from those of *Takapsestis* by their generally larger size, stronger ovipositor, well-developed, more or less rounded quadrangular penultimate tergite, broader tubular part of bursa, without swollen posterior part and by the larger, elliptical proximal part of bursae; the signum is absent or small in *Neotogaria*, that of *Chaeopsestis* long, ribbon-like.

Description. Small or medium-sized species (wingspan 32–42 mm) with relatively robust body. Head small, palpi elongate, slightly upturned, second segment rather slender, third segment medium-long or long, bar-shaped. Eyes rather small, globular, always hairy, with density and strength being different in the three subgenera. Antenna relatively long, lamellate in both sexes. Forewing narrow, elongate with apex pointed, hindwing small, rounded. Abdomen with dorsal tuft on third segment.

Male genitalia. Uncus and socii stick- or bar-shaped, always simple, their basal portions usually broad; ratio of length of uncus and socius being characteristic for species and subgenera. Fultura superior weakly sclerotized, most often long, narrow stripe, fultura inferior sclerotized, cup-shaped or subtriangular with stronger lateral arms, medial incision variably strong, its shape is a good specific character. Valva elongate, narrow, its apex always rounded. Sacculus relatively short, shorter than half length of valva, with stronger sclerotization along ventral margin. Terminal saccular process variably long, rounded or acute triangular, usually strongly sclerotized. Mesal saccular process most often rounded triangular, sometimes rugose; regularly strong, may be covered densely with minute hair-like spiculi. Aedeagus tubular, carina with strong, acute ventral hook; vesica short, membranous, recurved (horseshoe-shaped), most often with small, semiglobular subbasal diverticulum and with large field of small, spiniform cornuti, shape and size of cornuti field and cornuti being characteristic for subgenera.

Female genitalia. Ovipositor weak, short, conical, dorsal plate of penultimate segment (8th tergite) quadratic or V-shaped, with straight or with dentate margins. Ostium bursae infundibuliform, membranous, with large, rounded or narrow, slightly falcate antevaginal sclerites. Ductus bursae very short, finely sclerotized, cervical part of bursa copulatrix tubular, membranous, finely wrinkled and twisted, with more or less strongly dilated, swollen, verrucose and rugose posterior half of medial third. Corpus bursae elliptical or discoidal, its walls weakly membranous, signum always present, elongate, stripe-or bar-like, often interrupted, finely dentate or granulous.

Bionomics. The bionomical data of the species of the genus are rather heterogeneous. The members of the subg. *Takapsestis* are presumably univoltine early spring species, occurring at rather high elevations in mountainous deciduous forests, between 2000–3000 m a.s.l. in the Himalayan region and in Taiwan. The only exception is *T. fascinata*, a part of the known specimens (the two types)

of which were collected in June–July. The two subspecies of *T. (Neogaurena) semiobsoleta* are on wing at the late autumn–early spring and also from the summer, they are possibly bivoltine, while *T. (Neotakatogaria) curvicosta* flies in the wintertime, from November to March. The imagines are strong flyers, active during the night and come to light, but are not attracted to sugar baits.

All species appear as rare, and are known only by the adults, the early stages and foodplants are unknown.

Distribution. A south-east Asian genus, its species occur from the SW Himalayas (Pakistan) throughout the Himalayan chain to Yünnan, northern Indochina (Thailand, Vietnam), SE China (Kuatun) and Taiwan to the east and the western Indonesia (Sumatra, Java) to the south. The subgenera *Takapsestis* and *Neotakatogaria* are typically Palaearctic while *Neogaurena* is tropical, known only from higher mountains of Sumatra and Java. The distribution patterns of the Palaearctic species are partly overlapping, although the number of the known localities of each species is very small.

Subgenus *Takapsestis* MATSUMURA, 1933

Diagnosis. The species of the subgenus *Takapsestis* differ externally from the taxa of the two other subgenera by their narrower, more elongate forewing, resembling often also certain species of *Neoploca*, *Demopsestis*, *Achlya* and *Epipsestis*. The eyes are densely hairy with long, fine hairs; the second joint of the labial palp is almost straight, medially slightly thickened; the third joint is long, bar-shaped, considerably longer than in the species of the two other subgenera.

The male genitalia of *Takapsestis* s. str. can be characterized by the nearly equally long uncus and socii, being regularly thicker than in *Neogaurena* and *Neotakatogaria*. The saccular part of the valva is stronger in sclerotization, the mesal process is significantly smaller than the terminal process, its surface is smooth, lacking the covering of tiny spiculi. The cornuti field of the vesica is very dense, more or less quadratic, consisting of fine, spiniform cornuti.

The female genitalia of *Takapsestis* s. str. differ from those of *Neogaurena* and *Neotakatogaria* by their characteristically V-shaped dorsal plate of the eighth segment and the larger, strongly dilated, more strongly sclerotized posterior third of the cervical part of bursa copulatrix (this part is less dilated, weaker in the other two subgenera, representing the medial third of of the tubular cervical part). In addition, the lateral sclerotization of the ostium bursae is separated into two distinct bars in *Takapsestis* s. str., this plate is continuous but narrow in *Neotakatogaria,* while it is broad, horseshoe-shaped and weakly sclerotized in *Neogaurena*.

Taxonomy. The subgenus contains four species, one of them is represented by two geographic subspecies. These taxa form three well-separable species-groups, *T. (T.) wilemaniella* and its subspecies resembles mostly the species of *Neoploca* or *Demopsestis*, *T. (T.) orbicularis* looks mostly like an *Achlya*, while the *T. (T.) bifasciata–fascinata* pair of species are similar to certain *Epipsestis* species. The

problems of the taxonomic interpretation of the known species can be derived from the small number of specimens available for the studies, the great individual variability of the taxa and the unfortunate, often misleading conditions of the type material, especially of *T. (T.) bifasciata*.

Takapsestis (Takapsestis) wilemaniella wilemaniella MATSUMURA, 1933 (Figs 23–25, 64, 72)

Takapsestis wilemaniella MATSUMURA, 1933, *Insecta matsumurana* **7**: 199, pl. 4, figs 5, 33. Type-locality: [Taiwan] Formosa, [Puli] Horisha.

[Synonymy: *Polyploca albibasis* WILEMAN, 1914, *Entomologist* **47**: 322. Type-locality: [Taiwan] Formosa, [Alishan Mt.] Arizan; preocc. by HAMPSON, [1893].]

Type material examined. The original picture (and text) of *Takapsestis wilemaniella*; the holotype of *Polyploca albibasis*, female, "red ring type label", "Formosa, Arizan, 23.III. A. E. Wileman 1913–180", "Polyploca albibasis sp. n. type" (with handwriting), gen. prep. No.: BM.77.

Additional material examined. 169 specimens, from various localities of Taiwan.

Gen. prep. Nos: males: LG494 (W5486), LG772 (W5342), LG493 (W5487); females: LG773 (W5343), LG1329 (W5639).

Taxonomy. The species was originally described by WILEMAN (1914) under the name *Polyploca albibasis*, which is the homonym of *Polyploca albibasis* HAMPSON [1893] (now belongs to the genus *Euparyphasma* FLETCHER, 1979). The species has long been considered as endemic to Taiwan, it was recently discovered in northern Vietnam, eastern Nepal, an additional specimen was found in the HÖNE material from SE China. These three populations differ conspicuously from each other by their external appearance (size and colouration of forewing), displaying no geographic tendencies from Taiwan to E Nepal, therefore they are considered as distinct geographic subspecies.

Diagnosis. The species is easily distinguishable from the other taxa of the subgenus by its more gracile, *Demopsestis*-like body, bright silvery forewing colouration and the brownish suffusion of the basal area between the subbasal and the antemedial lines. This species has the smallest individual variation of the external features within the subgenus.

The best distinctive feature of the male genitalia can be found in the ratio of length of the socius and uncus and the shape of the apical third of uncus. In *T. wilemaniella* the socius-uncus ratio is about 2/3 and the apical part of the uncus is slightly dilated with apex rounded, in *T. orbicularis* this is 3/4 and the uncus is cuneate with apically tapering tip, in the *T. fascinata* – *T. bifasciata* species-pair the ratio is about 1/1 (and both the uncus and the socii are shorter and thicker) and the tip of uncus is slightly angular.

The key feature of the female genitalia of *T. wilemaniella* is the dentate margins of the V-shaped eighth tergite, while they are straight in the other three species.

The distinctive features of the three subspecies of *T. wilemaniella* are discussed in the diagnoses of the following two taxa.

Description. Wingspan 36–38 mm, length of forewing 17–18 mm. Head small, palpi elongate, slightly upturned, third segment long, bar-shaped. Frons, collar, tegulae and mesothorax varies from pale ochreous brown to dark grey-brown, other parts of thorax and abdomen greyish. Forewing narrow, costal margin convex, apex pointed, outer margin evenly arcuate. Ground colour shiny silvery grey, irrorated with a few dark brownish scales, outer part of basal area between subbasal and antemedial lines suffused with light brown. Subbasal line arcuate, often obsolescent; antemedial and postmedial lines sharply defined, fine, simple, blackish, latter often defined with brownish outwards. Orbicular and reniform stigmata less distinct, finely encircled with dark grey, filled with ground colour. Subterminal well-marked, interrupted, consisting of blackish dots. Sexes similar, antenna of female slightly finer, narrower, abdomen may be rather thick in both sexes.

Male genitalia (Fig. 64). Uncus and socii long, stick-like, apical part of uncus slightly dilated with rounded tip, ratio of socius/uncus/ is about 2/3. Fultura superior weakly sclerotized, ribbon-like, fultura inferior V-shaped, with deep medial incision, lateral arms equally broad from tip to base. Valva elongate, its tip finely rounded, ventral margin angled inwards above terminal process of sacculus. Sacculus strong, rather long, with two processi, terminal process always stronger, longer, more acute than mesal process.

Female genitalia (Fig. 72). Dorsal plate of penultimate segment (8th tergite) V-shaped with dentate margins and sclerotized, pointed anterior extremity. Ostium bursae membranous, infundibuliform, with narrow, slightly falcate, antevaginal sclerites. Ductus bursae very short, finely sclerotized, signum elongate, ribbon-like, consisting of disjunct patches.

Bionomics and distribution. A univoltine early spring species being characteristic of the higher montane forest regions of Taiwan, appearing mostly above 2000 m a.s.l., although it can be found also in lower elevations in cold and moist forests. The adults come readily to light, but have not been observed feeding on sugar.

Takapsestis (Takapsestis) wilemaniella continentalis ssp. n. (Figs 26–27, 73, 75)

Holotype. Female, "N-Vietnam 1600 m, Mt. Fan-si-pan (Nord) Cha-Pa, Primärurwald, 22°17' N 103°44' E, 25.–30.III.1995, leg V. Sinjaev & A. Schintlmeister, MUSEUM WITT" (coll. Museum Witt). Gen. prep. No. RL6442 (W5478).

Paratypes. 1 male, with the same data as the holotype; 1 male, Mt. Fan-si-pan 2250 m, 28-29.03.1995. leg V. SINJAEV & A. SCHINTLMEISTER (both specimens in coll. Museum Witt); 1 male, China, Kuatun (2300 m) 27°40'N, 117°40'E, J. KLAPPERICH, 18.3.1938. (Fukien), (coll. ZFMK); 1 male, Vietnam, Prov. Lao Cai, 2050 m, Fan-si-pan Mts, 5 km W Cat Cat, 103°49,291'E, 22°18,337'N, 15.III.1998, leg. L. PEREGOVITS & T. VÁSÁRHELYI (coll. HNHM).

Gen. prep. Nos: males: LG490 (W5477), LG484 (5476), RL6861.

Taxonomy. The northern Vietnamese and SE Chinese specimens differ slightly in their external appearance, but as they differ more conspicuously from both the Taiwanese and Nepalese populations, and as the Chinese population is represented by only a single male, the populations occurring in SE China and N Vietnam are considered here as belonging to the same geographic subspecies. The differences between the male genitalia of the three subspecies are very small, the differences are slightly more expressed in the females. According to this fact and as the holotype of the nominotypical *T. (T.) w. wilemaniella* is a female, the holotypes designated for the two new subspecies are also females.

Diagnosis. *T. (T.) w. continentalis* is the smallest within the subspecies of *T. (T.) wilemaniella*, wingspan 32–34 mm, length of forewing 15–16 mm. It differs from the nominotypical and the Nepalese populations by its paler, less shining brownish grey forewing ground colour, less intense brownish suffusion in the basal area and along the crosslines, and the generally paler dark markings; from the Nepalese subspecies by its much paler forewings colouration.

The male genitalia (Fig. 75) of the Vietnamese subspecies, as compared with those of *T. (T.) w. wilemaniella*, have somewhat shorter terminal saccular process and weaker angle of ventral margin of valva, the mesal saccular process is slightly larger, broader. In the female genitalia (fig. 73) the apical part of the V-shaped dorsal plate of the 8th segment is not sclerotized, the signum of corpus bursae is longer, more interrupted than those of the typical race.

Bionomics and distribution. The new subspecies is known, by the available data, from the Fan-si-pan Mts (N Vietnam) and from the rather remote SE Chinese Kuatun (not Kuangtung!); this latter locality is closer geographically to Taiwan than to the other area-patch of this subspecies. This distribution pattern is highly improbable and *T. (T.) w. continentalis* will presumably be discovered in other areas of south-eastern China during the more intense faunistic exploration of these areas.

The Vietnamese specimens were collected in the higher mountainous primary monsoonic forest zone, in a very early spring aspect, together with numerous overwintering Noctuidae and winter Geometridae species.

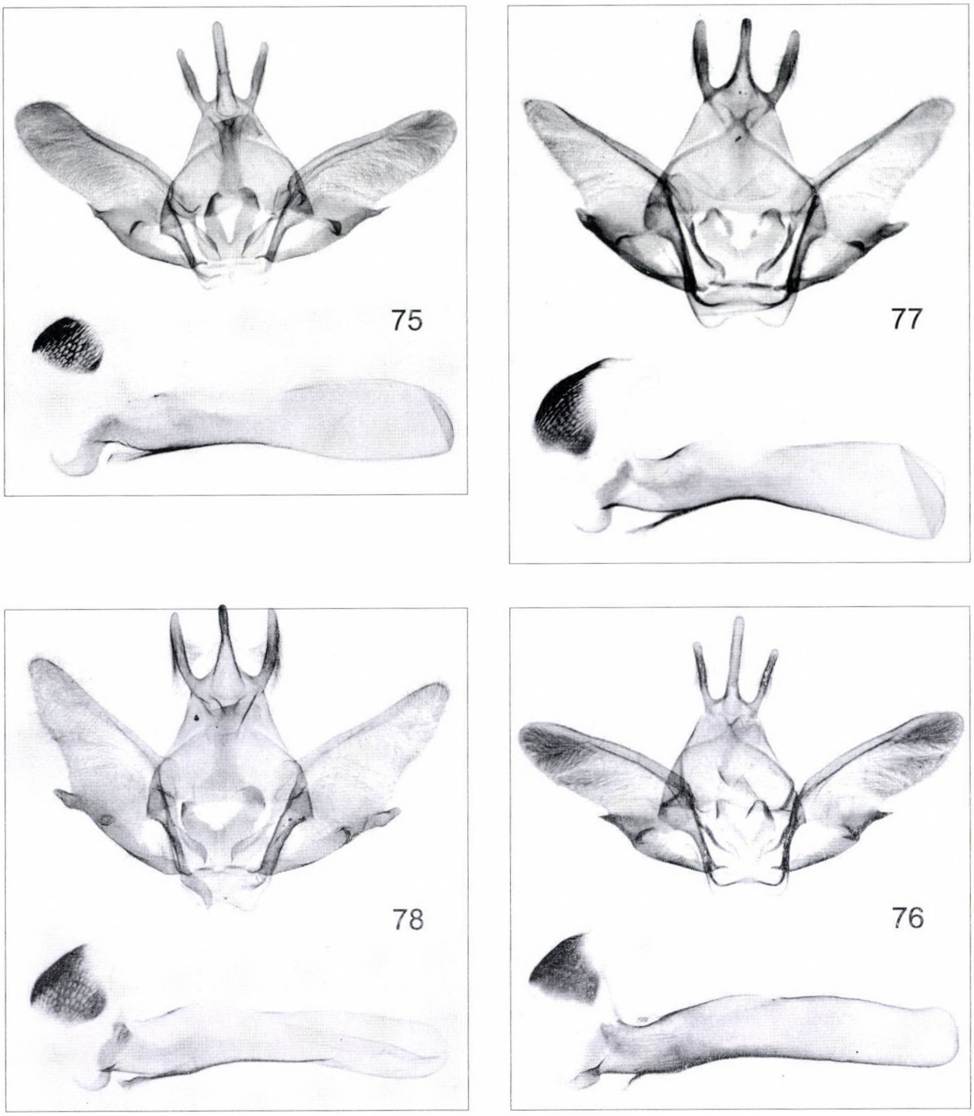
Etymology. The subspecific name refer to the first appearance of the species formerly considered as endemic to Taiwan on the continental part of Asia.

Takapsestis (Takapsestis) wilemaniella plumbeata ssp. n.
(Figs 28–29, 74, 76)

Holotype: female, "Nepal, Solu Khumbu, 1 km W of Ngomur, 3050 m, 14.03.1999, leg. Márton Hreblay, coll. Museum Witt". Gen. prep. No.: LG1317 (W5628).

Paratypes. 45 males and 43 females with same data as holotype (coll. Museum Witt).

Gen. prep. Nos: males: LG1315 (W5626), LG1316 (W5627); female: LG1318 (W5629).



Figs 75–78. Male genitalia apparatus of *Takapsestis (Takapsestis)* spp. 75 = *T. (T.) wilemaniella continentalis* ssp. n., paratype; 76 = *T. (T.) wilemaniella plumbeata* ssp. n., paratype; 77–78 = *T. (T.) bifasciata* (HAMPSON, 1895), Nepal

Taxonomy. The new subspecies was discovered surprisingly far to the west from the localities of the known populations of the species; it is known only from the Solu Khumbu Himal in E Nepal. The external differences between *T. (T.) w. plumbeata* and the other two taxa are rather conspicuous, but, as the genitalic differences between them are far less significant and the variation of the Nepalese population is poorly known (the whole material was collected on the same night!), it was more reasonable to interprete *plumbeata* as a subspecies of *T. (T.) wilemaniella*. On the other hand, the forthcoming exploration of the Nepalese Himalayan fauna will probably yield new material and hence solicit arguments for considering it as a distinct, allopatric species.

Diagnosis. The largest subspecies of *T. (T.) wilemaniella*, wingspan 37–40 mm, length of forewing 17–19,5 mm. It is easily distinguishable from the two other subspecies by its dark, less shining plumbeous grey forewing ground colour, the more intense dark brown fascia between the subbasal and antemedial lines, and the less conspicuous, often obsolete subterminal line. *T. (T.) w. plumbeata* can be separated from *T. orbicularis*, the other *Takapsestis* species occurring sympatrically with it in Nepal, by its more convex costal margin and smaller, narrower orbicular stigma.

In the male genitalia (Fig. 76), the terminal saccular process of *T. (T.) w. plumbeata* is shorter, the medial incision of the fultura inferior is deeper, more narrowly V-shaped than those of the other two races; in the female genitalia (Fig. 74), the V-shaped plate of the 8th tergite of *T. (T.) w. plumbeata* have longer, stronger sclerotized apical (anterior) extension (this extension is shorter, not or only weakly sclerotized in the two other subspecies). The ductus bursae of the Nepalese race is somewhat longer, stronger, the signum is shorter than those of *T. (T.) w. wilemaniella* and *T. (T.) w. continentalis*.

Bionomics and distribution. This subspecies was found only once in its type locality in a high montane *Rhododendron* forest, at the very early spring aspect.

Etymology. The subspecific name refers to its beautifully plumbeous grey forewing ground colour.

Takapsestis (Takapsestis) bifasciata (HAMPSON, 1895) (Figs 30–35, 77–78, 83)

Polyploca bifasciata HAMPSON, 1895, *Trans. ent. Soc. London* 1895: 281. Type-locality: India, Sikkim, Darjeeling.

[Synonymy: *Takapsestis nepalensis* YOSHIMOTO, 1992, *Tinea* **13**(suppl. 2): 48, pl. 13, fig. 12. Type-locality: Nepal, Godavari, **syn. n.**; *Takapsestis harutai* YOSHIMOTO, 1994, *Tinea* **14**(suppl. 1): 92, pl. 82, fig. 33. Type-locality: Nepal, Koshi, **syn. n.**]

Type material examined. Holotype female, "red ring type label", "Sikkim, 23.3.1889 Knyvett", "Elwes collectio Rothschild Bequest 1939-1", "Polyploca bifasciata female Hmps." (with handwriting); abdomen and gen. prep. No. missing.

Additional material examined. India: Sikkim. *Takapsestis bifasciata* ab. *confusa* (WARREN), male, "red ring type label", "Sikkim interior, Möller, type", "collectio H. J. Elwes, gen. prep. No.: BM. 145", "Polyploca bifasciata ab. confusa male WARREN" (with handwriting), (manuscript name). *Takapsestis bifasciata* ab. *declivis* (WARREN), male, "red ring type label", "Darjeeling, 7500 ft, May–June, 1889 A. V. Knyvett", "collectio H. J. Elwes", "Polyploca bifasciata ab. declivis type male Warren" (with handwriting) (manuscript name) (both specimens are in coll. BMNH).

Nepal. About fifty specimens from various places of the Annapurna Himal, Ganesh Himal, Solu Khumbu Himal and Kanchenjunga Himal.

Gen. prep. Nos: males: LG480 (W5473), LG492 (W5474), LG491(W5475), LG895 (W5553), LG1321 (W5632), LG 1322 (W5633); female: LG1320 (W5631).

Taxonomy. The species was originally described as *Polyploca bifasciata*. YOSHIMOTO has firstly transferred to it to *Epipsestis* (1982), and placed to *Takapsestis* one year later (1983), mentioning that he had the opportunity to study the photography of the type, which was published in both papers. He has described further three species of *Takapsestis, T. fascinata* from Yünnan (1990), *T. nepalensis* (1992) and *T. harutai* (1994) from Nepal. Unfortunately, the holotype of *T. bifasciata* is an aberrative specimen, its abdomen has been lost, therefore its genitalia cannot be studied, the additional material available from the species group is very small. This unlucky coincidence of problems could led to the result that *T. nepalensis* is fairly identical with *T. bifasciata*, and *T. harutai* is a pale, almost patternless form of the latter species.

We had the opportunity to study a larger material from Nepal, which contains a wide range of variation in colour and dark markings of the forewing, although none of them was completely matching with the holotype from this respect. It could be stated that there is a strongly polymorphic pair of species, *T. bifasciata* and *T. fascinata*, and the other described taxa represent only different forms of the former taxon. The extremes of both species can easily be considered as distinct taxa, especially if the intermediate forms are not in hand and the genitalic features are not studied carefully. The "*harutai* form" is very pale greyish with fine, weak crosslines, without stronger dark suffusion along ante- and postmedial lines, the stigmata are stronger, often filled with ochreous, the "*nepalensis* form" is regularly darker with broad, dark grey-brown fasciae along antemedial and postmedial lines.

It is worth to mention that the genitalia of *T. nepalensis* and *T. harutai* have been compared in the original description only with those of *T. orbicularis* and not with *T. fascinata*. YOSHIMOTO mentioned in the diagnosis of *T. harutai* that the

species is similar to that of *T. nepalensis*, especially in the male genitalia (the female of the *T. harutai* was unknown!), but he found differences in the thickness of the male antenna. The study of the antennae of several, externally strongly different males cannot confirm this statement, the measures of the antennae proved to be identical (possibly a curious procedure of setting could cause some differences?).

The pictures of the male genitalia of the types of *T. nepalensis* and *T harutai* display some slight differences in the shape and size of the valva, the saccular processi and the ventral hook of the carina. Comparing the series of male genital slides these features show rather strong variability and numerous intermediate stages, appearing in different combinations; one of the externally *nepalensis*-like specimen has the genitalia matching best with the genitalia of the paratype of *T. harutai*. On the other hand, the genitalia of *T. orbicularis* and *T. bifasciata* (=*nepalensis*, =*harutai*) really show clearly recognizable, although not very large differences.

Diagnosis. *T. bifasciata* is externally often hardly separable from its, by our recent knowledge entirely allopatric, sister species, *T. fascinata*, although *T. bifasciata* is usually much more variegated in ground colour and pattern of the forewing. The best external feature for their separation is the shape, colour and size of the orbicular and reniform stigmata: the orbicular stigma of *T. bifasciata* is larger, regularly round, often filled with ochreous-yellowish, that of *T. fascinata* smaller, more whitish coloured, sometimes rather large but not rounded, but forming a broad "8". The shape of the reniform is similar in the two taxa except the short extension at lower part, which is shorter, broader in *T. bifasciata*, longer, tapering in *T. fascinata*. The satisfactory identification, however requires the study of the genitalia.

The male genitalia of the two species are very similar by their equally long unci and socii; the key feature is the shape and size of the fultura inferior. The fultura inferior of *T. bifasciata* is smaller, with V-shaped medial incision and broad, apical arms, while the fultura inferior of *T. fascinata* is larger, broader at base, its shape is charateristically calyciform with much larger, U-shaped incision and narrow, fine apical arms.

In the female genitalia the finely sclerotized, swollen part of the posterior third of the cervical part of bursa copulatrix is larger, longer in *T. bifasciata* and the signum is finer, somewhat shorter.

Description. Wingspan 35–38 mm, length of forewing 17–18 mm. Pubescence of head, collar and tegulae greyish brown, mixed with ochreous brown hairs, collar with fine, blackish subapical stripe. Abdomen paler, dorsal crest represented by large tuft on 3rd segment. Forewing elongate, narrow, with apex finely pointed, ground colour paler or darker grey or brownish grey, with variably strong blackish irroration. Intensity of forewing pattern extremely variable, crosslines may be fine, simple or stronger, more or less double, sometimes with broad, dark brown or blackish brown fasciae. Distinctness and colouration of orbicular and reniform stigmata also variable, their filling often

ochreous or yellowish. Orbicular rather large, rounded, reniform narrow, lower part slightly dilated towards inner area of cell.

Male genitalia (Figs 77–78). Uncus and socii nearly equally long and thick, stick-like. Fultura inferior rather broad, with deep V-shaped medial incision and wide apical arms. Valva elongate, apically finely rounded, saccular lobe strongly sclerotized; ventral margin of valva not angled above distal end of sacculus. Terminal saccular process variably long, acute, wedge-shaped, mesal process broad-based, small, rounded apically.

Female genitalia (Fig. 83). Ovipositor short, papillae anales apically rounded, posterior apophyses long, slender. 8th tergite trigonical, with straight lateral edges, its tip pointed. Antevaginal plates strong, sclerotized, with rounded proximal margins, disjunct at ostial ring. Ostium bursae membranous, ductus bursae very short, sclerotized. Posterior third of cervical part of bursa copulatrix finely sclerotized, swollen, wrinkled, corpus bursae large, elliptical; signum long, ribbon-like.

Bionomics and distribution. A typically early spring species, occurring on the higher deciduous forest zones of the southern Himalayas; it is recorded from Central Nepal (Annapurna Himal, Godavari, Ganesh Himal, Solu Khumbu Himal) and Sikkim (Nepal: Kanchenjunga Himal; India: Darjeeling). Only a few specimens are known, all were collected at light; the early stages and the larval foodplant are unknown.

Remarks. The literature data of the original description are erroneously cited by YOSHIMOTO (1983) as "1896" and "*The Fauna of British India* 4: 463."

The sex of the holotype is mentioned in the original description as "male" (?lapsus calami), but labelled as "female".

There are two specimens designated but undescribed by WARREN as types of aberrations of *T. bifasciata*. These specimens represent two different stages between the *nepalensis* and *harutai* forms.

Takapsestis (Takapsestis) fascinata YOSHIMOTO, 1990 (Figs 36–38, 79–80)

Takapsestis fascinata YOSHIMOTO, 1990, *Nota lepid.* 13(4): 236. Type-locality: China, Yünnan, A-tun-tse.

Type material examined. The pictures (the moth and the genitalia of both sexes) in the original description.

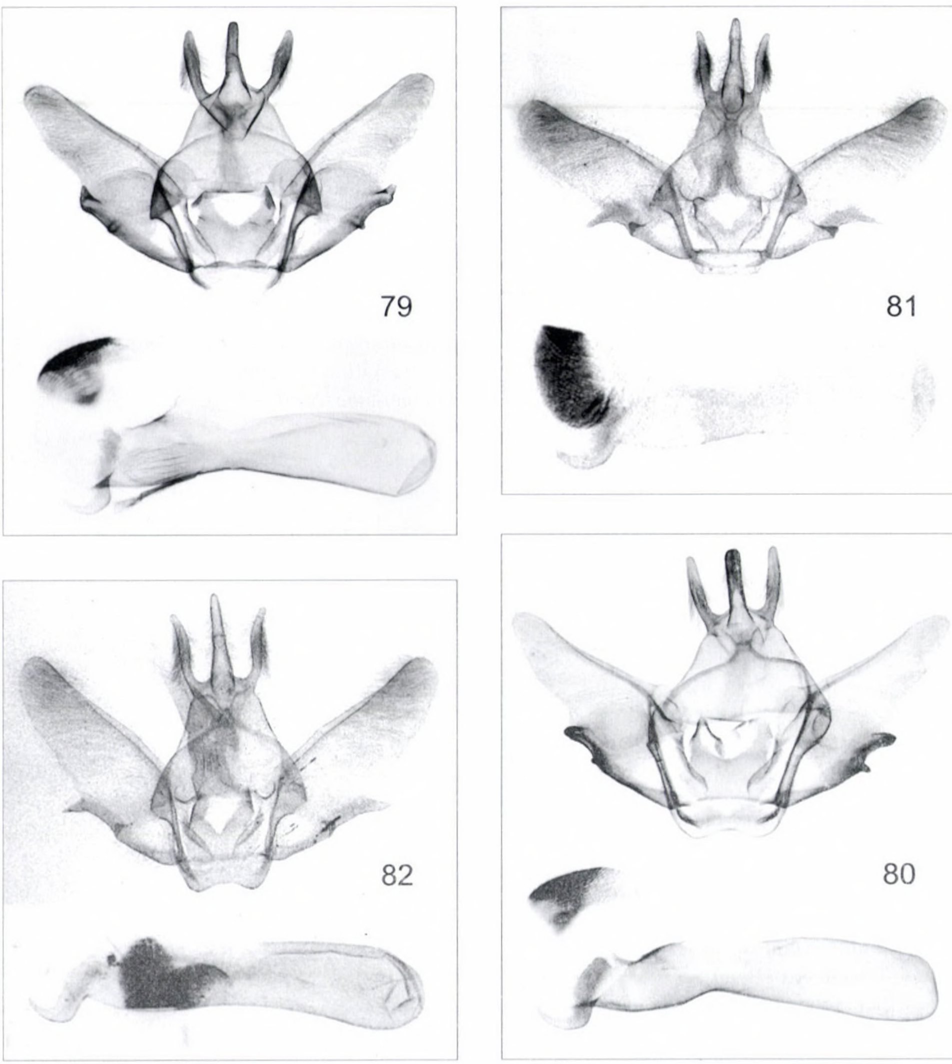
Additional material examined. N Vietnam: 2 males, Prov. Lao Cai, 2450 m, Fan-si-pan Mts, 6 km W of Cat Cat 22°18'N, 103°65'E, 14.III.1998, leg. PEREGOVITS et VÁSÁRHELYI (coll. HNHM). China: 7 males, Yünnan, 5 km N of Hutiaoxia, 220 km N. Dali, 2200 m, 23-27.IV.1998, ex coll. Dr. R. BRECHLIN (coll. Museum Witt).

Gen. prep. Nos: males: RL6339, RL6857, RL6858, RL6859.

Taxonomy. The two known populations from North Yünnan and northern Vietnam show no distinctive features, therefore the species is considered as homogeneous from taxonomic point of view.

Diagnosis. Probably the most variable species of the genus, allied closely to *T. bifasciata*. The detailed comparison of the two species is given in the diagnosis of the preceding taxon.

Description. Wingspan 36–38 mm, length of forewing 16–18 mm. Vestiture of head and thorax variably dark brownish grey mixed with ochreous brown and a few blackish hairs, collar with



Figs 79–82. Male genitalia apparatus of *Takapsestis (Takapsestis)* spp. 79–80 = *T. (T.) fascinata* YOSHIMOTO, 1990, 79 = Vietnam, 80 = China, Yünnan; 81–82 = *T. (T.) orbicularis* (MOORE, 1888): 81 = holotype of *Polyploca griseata* WARREN, 1915, 82 = lectotype, male

black line, abdomen with large blackish tuft on 3rd segment. Forewing elongate, ground colour strongly variable from pale whitish grey to dark brownish grey, with often rather strong darker grey and/or blackish irroration. Forewing pattern highly variable, antemedial and postmedial crosslines may be weak, fine, simple or strong, more or less double, or even defined with broad, dark brown or blackish brown fasciae. Orbicular and reniform stigmata rather conspicuous, their filling often clear white. Orbicular relatively small, rounded or larger, with shape of "8", reniform narrow, lower part with longer, tapering extension projecting towards inner area of cell.

Male genitalia (Figs 79–80). They are very similar to those of *T. bifasciata* with their nearly equally long and thick, stick-like uncus and socii and the shape of the valva and the saccular processi. Fultura inferior broad, broader at base than apically, more or less calyculate with deep U-shaped incision and fine, narrow apical arms.

Female genitalia. They are matching well with those of *T. bifasciata*, showing slight differences in the size of the swollen part of the posterior third of the cervical part of bursa copulatrix and the signum.

Bionomics and distribution. The species is known only by two rather disjunct, but not very remote areas, from N Yünnan (A-tun-tse and Hutiaoxia) and from the Fan-si-pan Mts, the highest mountain of Indochina. The two types were collected in summer, all newly found specimens originate from the early spring. The material available is insufficient to decide whether this species has two distinct generations or the species is univoltine with a longer, rather asynchronous hatching period. According to the other taxa of the subgenus, the univoltine life cycle is more probable. The known specimens were collected in the monsoonic high montane forest zone between 2200–3000 m a.s.l. Early stages and foodplant are unknown.

Takapsestis (Takapsestis) orbicularis (MOORE, 1888) (Figs 39–42, 81–82, 84)

Palimpsestis orbicularis MOORE, 1888, *Proc. zool. Soc. London* 1888: 407. Type-locality: India, Kangra district, Dharmsala.

[Synonymy: *Polyploca griseata* WARREN, 1915, *Novitates zool.* 22: 157. Type-locality: NW-India, Kangra district, **syn. n.**]

Type material examined. Syntypes of *Takapsestis orbicularis*: male, "red ring type label", "Dharmsala", gen. prep. No.: BM.133; female, "red ring type label", "Dharmsala". The male syntype of *T. orbicularis* is designated here as lectotype, the female is a paralectotype (both specimens are in coll. BMNH).

Holotype of *Polyploca griseata* WARREN, male, "Kangra, Hocking. Elwes coll.", "probably holotype, 31.dec.1971, M. Grogan" (with handwriting); gen. prep. No.: BM.62. (coll. BMNH).

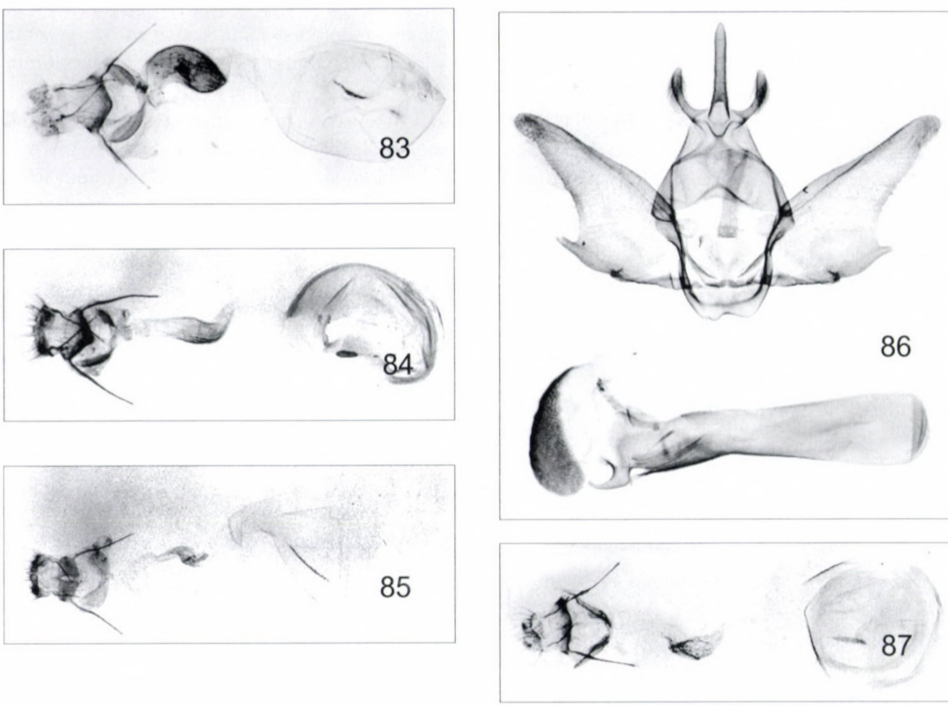
Additional material examined. 27 specimens from C Nepal (Ganesh Himal, Annapurna Himal, Dhaulagiri Himal); 5 specimens from N Pakistan (Indus valley and Swat).

Gen. prep. Nos: males: LG478 (W5468), LG479 (W5469), LG481 (5470), RL6466 (W5467), RL6860, LG1319 (W5630); females: LG780 (W5350), RL6867.

Taxonomy. The species was originally described by two syntypes, the male syntype is designated here as lectotype. No subsequent records have been pub-

lished after the description of the taxon. The Pakistani population, one of the newly discovered ones, show some external differences when compared with the others occurring in Himachal Pradesh and in Central Nepal, in addition, their habitats differ also from those of the south Himalayan populations. On the other hand, this species has a considerable range of variation in its external features and the configuration of the genitalia is rather conservative. Thus, the small material available cannot serve as a good basis for satisfactory microsystematic analysis and the different populations are interpreted here as representing the same subspecific unit.

Diagnosis. The largest species of the subgenus, resembling also certain *Achlya* species. It can relatively easily be distinguished from the related taxa by its more robust body, longer, narrower forewings with less intense dark pattern and larger, round orbicular stigma. In the male genitalia the socii are shorter than the uncus, not more or less equally long as in the *T. bifasciata–T. fascinata* species pair and



Figs 83–87. Genitalia apparatus of *Takapsestis* spp. 83 = *Takapsestis (Takapsestis) bifasciata* (HAMPSON, 1895) Nepal, female; 84 = *T. (T.) orbicularis* (MOORE, 1888), Nepal, female; 85 = *T. (Neogaurena) semiobsoleta semiobsoleta* (WARREN, 1915), Java, female; 86–87 = *T. (Neotakatogaria) curvicosta* (WARREN, 1915), 86 = holotype, male; 87 = Thailand, female

are finer, more slender. The medial incision of the fultura inferior is narrower, with broader arms; the terminal saccular process is the longest within the related taxa; the ventral margin of the valva is not angled inwards above the distal end of sacculus.

The female genitalia of *T. orbicularis* differ from those of *T. bifasciata* and *T. fascinata* by the V-shaped 8th tergite, having straight lateral arms, the narrow, weakly sclerotized lamellae antevaginales, the membranous ostium bursae and the longer but less sclerotized swollen posterior third of cervical part of bursa copulatrix.

Description. Wingspan 39–41 mm, length of forewing 19–20 mm. Body rather strong, pubescence of head and thorax dark brownish grey or plumbeous grey mixed with paler grey and a few blackish hairs. Forewing elongate, narrow, with apex pointed, ground colour variable, most often dark grey with intense blackish irroration. Wing pattern variably strong, well-marked form has fine, sharp, black(ish) antemedial and postmedial crosslines, defined usually with brownish fasciae; basal field with variably intense brownish suffusion between subbasal and antemedial lines. Orbicular stigma regularly large, round, filled with paler grey or ochreous scales, reniform narrow, straight, filled with ground colour, lower third with blackish inner dot. Less marked form (= *griseata* WARREN) has usually unicolorous dark grey ground colour with indistinct, often obsolete crosslines, but rather conspicuous, large, ochreous orbicular stigma.

Male genitalia (Figs 81–82). Uncus and socii stick-like, socii shorter than uncus, their ratio of length is 3/4. Fultura inferior rather narrow at base, apically deeply incised forming a large but relatively narrow V, having long, relatively broad arms. Valva elongate, apically rounded, without stronger ventral angle at distal end of sacculus. Sacculus strongly sclerotized, terminal process strong, long, acute, mesal process small, narrow, its tip projecting to tip of terminal process.

Female genitalia (Fig. 84). Ovipositor short, papillae anales small, narrow, apically rounded, apophyses posteriores long, slender. 8th tergite trigonical with straight margins and pointed proximal tip. Lamellae antevaginales forming two narrow, elongate quadrangular, sclerotized plates along lateral sides of membranous, infundibuliform ostium bursae. Ductus bursae very short, weakly sclerotized, posterior third of cervical part of bursa copulatrix swollen, slightly folded, with fine sclerotization; signum ribbon-like, interrupted, narrow, with relatively large distal (caudal) patch.

Bionomics and distribution. The species has a rather scattered area in the south-western and southern Himalayan massif from Pakistan throughout Himachal Pradesh to Central Nepal. The southern Himalayan populations inhabit the high and very high monsoonic deciduous forest zones between 2500–3500 m altitudes, the Pakistani specimens were found in rather low and medium high regions in the remnants of the hard-leaved, shrubby oak forest zone. The life cycle is univoltine, the adults are on wing in April–May and are attracted to artificial light. The early stages and the foodplant are unknown.

Remarks. YOSHIMOTO (1990) has also expressed his opinion on the possible synonymy of *T. griseata* with *T. orbicularis*.

Subgenus *Neogaurena* ROEPKE, 1944, **stat. n.**

Diagnosis. The species belonging to the subgenus *Neogaurena* has rather short, broad forewings; the eyes are more scarcely hairy and these hairs are finer than those of *Takapsestis* and *Neotakatogaria*; can often be observed only in larger magnification. The second joint of the labial palp is almost straight, the third joint is shorter than in *Takapsestis*.

The male genitalia of *Neogaurena* differ mostly from the species of *Takapsestis* s. str. by its long, slender uncus, being more than twice as long as the socii. The saccular part of the valva is rather weak in sclerotization, the mesal process is the strongest within the genus, larger, stronger than the terminal process, covered densely with fine, tiny spiculi. The ventral hook of the carina is finer but longer than in the other two subgenera, the cornuti field of the vesica is more elongate, narrower, consisting of larger, thorn-like cornuti.

The female genitalia of *Neogaurena* s. str. have broad, quadrangular dorsal plate of the eighth segment, the postvaginal lamellae are broad, rounded and the tubular cervical part of the bursa copulatrix is longer, narrower, the dilated, more sclerotized part is small, rather weak, situated at the medial third of the tube.

Takapsestis (Neogaurena) semiobsoleta semiobsoleta (WARREN, 1915) (Figs 43–44, 85, 88)

Palimpsestes (sic!) *semiobsoleta* WARREN, 1915, *Novitates zool.* 22: 156. Type-locality: Java, Pengalengan.

[Synonymy: *Neogaurena grisescens* ROEPKE, 1944, *Natuurh. Maandblad* 33: 65. Type-locality: Java, Potachawattee.]

Type material examined. Holotype male, "red ring type label", "Pengalengan Preanger", "*Polyploca semiobsoleta* type male Warren" (with handwriting), gen. prep. No.: BM.68. (coll. BMNH).

Additinal material examined. 5 males, 1 female, Java, Mt. Pangrange, 30 km SE Bogor, 1625 m, primary forest, 6°30'S, 107°10'E, 6–20.2.1996, leg. SINAJEV & AFONIN (coll. Museum Witt). Gen. prep. Nos: male: LG495 (W5471), female: RL6868.

Taxonomy. The species has two fairly isolated geographic subspecies, the ssp. *semiobsoleta* occurs in Java, the ssp. *sumatrensis* lives in Sumatra. This latter taxon was originally described as a form of *T. orbicularis* and treated as a full species by YOSHIMOTO (1983). He has recognized the close relationship between *T. semiobsoleta* and *T. sumatrensis*, but separated them on specific level by the hairiness of the eyes: he has stated that the eyes of *T. semiobsoleta* are naked while

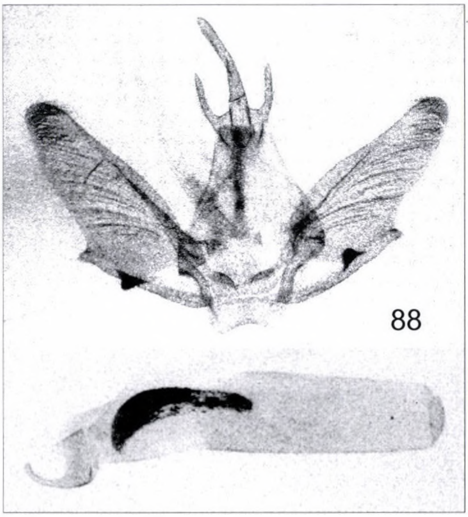
those of *T. sumatrensis* are finely hairy. The specimens of both populations studied have finely hairy eyes, no remarkable differences were found neither in this feature nor the genitalia of both sexes. As the imagines of these two populations differ in some external features and are clearly isolated from each other, they are considered as two geographic races of the same species.

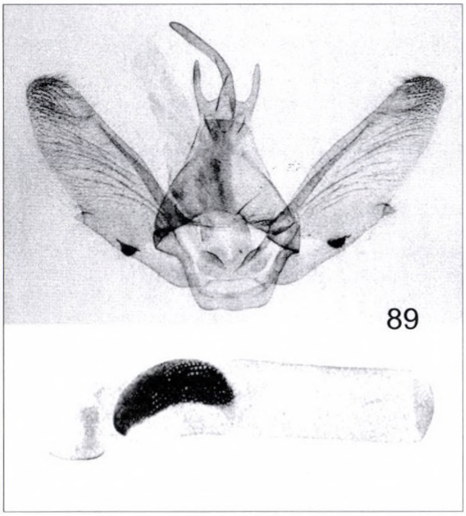
T. semiobsoleta was described again by ROEPKE (1944) as a member of a new genus, *Neugaurena grisescens*, this taxon was synonymized with *T. semiobsoleta* by YOSHIMOTO in 1990.

It is worth to mention that the holotypes of the two taxa are the most divergent specimens we had the opportunity to study: the holotype of *semiobsoleta* is the smallest and most unicolorous specimen we have ever seen, while the holotype of *sumatrensis* is a large, contrasty moth. The great colour variation of the species can also be found in the Javan population.

Diagnosis. The diagnostic features of the species are discussed in detail in the diagnosis of the subgenus; the differences between the two subspecies are given under *T. semiobsoleta sumatrensis*.

Description. Wingspan 32–36 mm, length of forewing 15–18 mm. Rather strongly built moths, pubescence of head and thorax regularly greyish brown mixed with ochreous hairs, collar with fine subapical black line. Forewing relatively short, broad, with apex pointed, ground colour greyish brown, irrorated variably strongly, but often intensely with brown and a few blackish scales.





Figs 88–89. Male genitalia of *Takapsestis (Neogaurena) semiobsoleta*. 88 = *T. (N.) s. semiobsoleta* (WARREN, 1915), holotype, male; 89 = *T. (N.) s. sumatrensis* (GAEDE, 1930), holotype, male

Crosslines present, fully marked but usually fine, blackish grey; median area narrow, lightest part of wing. Orbicular stigma always whitish, regularly larger than darker greyish reniform.

Male genitalia (Fig. 88). Uncus long, slender, twice as long as socii. Fultura superior narrow, long, bar-like; fultura inferior deeply incised medially. Valvae elongate, apically rounded, saccular part rather weak in sclerotization, mesal process strong, with rounded tip, larger, stronger than terminal process, covered densely with fine, tiny spiculi. Aedeagus with fine, long ventral hook of carina, vesica with long, narrow cornuti field, covered with rather strong, thorn-like cornuti

Female genitalia (Fig. 85). Papillae anales finely rounded, 8th tergite sclerotized, broad, quadrangular. Ostial plates forming broad, U-shaped lamella, ostium bursae membranous, funnel-like; tubular cervical part of bursa copulatrix partly wrinkled, its proximal third finely sclerotized. Corpus bursae more or less bottle-shaped, proximally slightly angular; signum long, narrow, ribbon-like.

Bionomics and distribution. The nominotypical race appears as endemic to Java. It is presumably univoltine, the few known examples were collected in February. The early stages and the foodplant are unknown.

Takapsestis (Neogaurena) semiobsoleta sumatrensis (GAEDE, 1930), **stat. n.** (Figs 45–46, 89)

Polyploca orbicularis f. *sumatrensis* GAEDE, 1930, *in* SEITZ: *Gross-Schmetterlinge der Erde*, 10: 661, pl. 85, row c. Type-locality: Sumatra, Khorintji Mt.

Type material examined. Holotype male, "red ring type label", "Sumatra 7. 22. Slopes of Mt. Khorintji, 7300 ft., aug.-sept. 1921. C., F., & J. Pratt", gen. prep. No.: BM.92. (coll. BMNH).

Additional material examined. 1 male, "Sumatra 7. 22. Slopes of Mt. Khorintji, 7300 ft., aug.-sept. 1921. C., F., & J. Pratt", "id. mit Type sumatrensis, gute Art Gaede" (with handwriting), "abdomen missing" (with handwriting) (coll. BMNH); 1 male, N-Sumatra, Deli Dolok Merangir, 180 m, 1973, leg. E. DIEHL (coll. ZSM).

Taxonomy. The taxon was originally described by GAEDE (1930) as a form of *T. orbicularis*. It was upgraded to species rank by YOSHIMOTO in 1983.

Neogaurena grisescens was erroneously mentioned by HOLLOWAY (1998) as a new synonym of *T. sumatrensis* (GAEDE, 1930) although it is a synonym of *T. semiobsoleta* and not of *T. sumatrensis* and this synonymy has already been clarified by YOSHIMOTO (1990).

Diagnosis. The Sumatran population differs from the more unicolorous nominotypical subspecies from Java by its more conspicuous forewing pattern and more variegated colouration with lighter median area. The shape and size of the forewing are similar to that of *T. semiobsoleta*, wingspan 35–39 mm, length of forewing 17–19 mm.

The small differences observable in the genitalia of the two holotypes can be considered as different stages within the range of variation of the same species.

It is worth to mention that the phaenology of the two taxa are different: the known specimens of *T. s. semiobsoleta* were collected in February while those of *T. s. sumatrensis* are on wing in the summer period. It is not impossible that this phenomenon is a consequence of the small material available and the flight period of the two subspecies is similarly bimodal.

Bionomics and distribution. Appears as endemic to Sumatra, the few known imagines were collected in different forested areas of the island.

Subgenus *Neotakatogaria* **subg. n.**

Type-species: *Polyploca curvicosta* WARREN, 1915, *Novitates zool.* 22: 156. Type-locality: India, Khasis.

Diagnosis. The only known species of the subgenus *Neotakatogaria* is easily distinguishable from the other *Takapsestis* species by its strongly convex forewing costa and the *Neotogaria*-like forewing pattern with sharply defined, black apical streak, ante- and postmedial crosslines and orbicular and reniform stigmata.

The most conspicuous difference between the male genitalia of *Neotakatogaria* and *Takapsestis* s.str. is the size and rate of the uncus and the socii: the uncus is long, slender, being more than twice as long as the socii. Another distinctive feature is the length of the terminal saccular process, that of *Neotakatogaria* is the longest within the genus; in addition, the cornuti of the vesica are the smallest, compared with those of *Takapsestis* s.str. and *Neogaurena*.

The unique feature of the female genitalia of *Neotakatogaria* is the narrow, quadrangular 8th tergite. The postvaginal plates are fused into a joint lamina like in *Neogaurena*, this lamina is narrower than that of *T.* (*Neogaurena*) *semiobsoleta,* while *Takapsestis* s.str. has distinct postvaginal plates.

Description. Monotypic subgenus, its species has characteristically strongly convex costal margin of the forewing with *Neotogaria*-like forewing pattern. The eyes are small, rounded, only slightly hairy; the second joint of the labial palp is finely arcuate, covered with erected hair-scales; the third joint is long, slender.

The male genitalia (Fig. 86) of *Neotakatogaria* have rather thick uncus and socii like in *Takapsestis* s. str., but the ratio of their length is similar to that of *Neogaurena*. The ventral margin of the valva is conspicuously arcuate, the saccular part is strongly sclerotized, the mesal process is rather weak, finely rugulose, covered with minute, hair-like spiculi; the terminal process is long, slender, pointed. The ventral hook of the carina is finer, relatively short, the cornuti field of the vesica is large, very dense, the cornuti are the smallest within the genus.

In the female genitalia (Fig. 87) of *Neotakatogaria* the dorsal plate of the eighth segment is narrow, quadrangular (half-ring-like), the ostium bursae is calyculate, finely scobinate, with short,

weak, finely arcuate postvaginal lamellae; the tubular cervical part of the bursa copulatrix has small, but rather strong sclerotized part, situated at the medial third of the tube.

Takapsestis (Neotakatogaria) curvicosta (WARREN, 1915) (Figs 47–48, 86–87)

Polyploca curvicosta WARREN, 1915, *Novitates zool.* 22: 156. Type-locality: India, Khasis.

Type material examined. Holotype male, "red ring type label", "Khasis, Nov. 1896 Nat. coll.", "Polyploca curvicosta type male Warr." (with handwriting), gen. prep. No.: BM.141. (coll. BMNH).

Additional material examined: Thailand: 1 male, Prov. Chiang Mai, 20km NW of Mae Ai, 1650 m, 16.12.1998, leg. M. HREBLAY, Y. SHERPA et I. SOÓS; 3 males and 1 female, Mt. Doi Phahampok, 18 km NW of Fang, 2000 m, 10.01.1999; 4 males, Mt. Doi Phahampok, 18 km NW of Fang, 2100 m, 09.01.1999; 1 male, Mt. Doi Inthanon NP, 2300 m, 21.01.1999, leg. SZABÓ et CZERE (coll. Museum Witt).

Gen. prep. Nos: male: LG689 (W5240), female: RL6862.

Taxonomy. The taxonomic combination of the species was correctly stated firstly by YOSHIMOTO (1990).

Description. Wingspan 31–32 mm, length of forewing 14–15 mm. Forewing elongate, distally broadened with characteristically strongly convex costal margin. Ground colour mouse-grey or pale graphite-grey, basal area irrorated with brown, with diffuse darker fasciae. Antemedial and postmedial crosslines sharply defined, double, blackish, median area very narrow. Orbicular stigma small, elliptical, straight, reniform oblique, drop-shaped, extending inwards below reniform. Both stigmata encircled with blackish, filled with darker grey. Subterminal line with sharply defined, blackish or dark graphite-grey apical streak and interrupted, sometimes obsolescent lower part.

The characterization of the genitalia and the diagnosis are given in the paragraphs of the subgenus *Neotakatogaria*.

Bionomics and distribution. A poorly known species, only a few records are known from northern India (Khasia Hills), Central Nepal (a single specimen from Jiri, YOSHIMOTO, 1994) and from Northern Thailand. A most probably univoltine winter species, the flight period extends from November to March.

*

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REFERENCES

DALLA TORRE, K. W. (1921) Cymatophoridae. *In:* Junk, *Lepidopterorum Catalogus* **25**: 1–38.

FLETCHER, D. S. (1979) *The generic names of moths of the world*, III. British Museum (Nat. Hist.), London, 243 pp.

FORBES, W. T. M. (1936) The classification of the Thyatiridae (Lep.). *Annls ent. soc. Am.* **29**: 779–803.

GAEDE, M. (1930) Cymatophoridae. *In*: SEITZ, A.: *Die Gross-Schmetterlinge der Erde,* Vol. 10, Stuttgart, pp. 658–663, pl. 85.

HAMPSON, G. F. (1893) *Fauna of British India, Moths,* Vol. 1, London, 527 pp.

HAMPSON, G. F. (1896) *Fauna of British India, Moths,* Vol. 4, London, 594 pp.

HOLLOWAY, J. D. (1998) The Moths of Borneo: Families Castniidae, Callidulidae, Drepanidae and Uraniidae. *Malayan Nature J.* **52**: 1–155.

HOULBERT, C. (1921) Revision monographique de la famille des Cymatophoridae. *In* Oberthür, XXX: *Études de Lépidopterologie Comparée* **18**(2): 23–252.

KOBES, L. W. R. (1985) The Thyatiridae, Agaristidae and Noctuidae (Part I: Pantheinae and Catocalinae) of Sumatra. *Heterocera Sumatrana* **4**: 1–92.

MATSUMURA, S. (1921) *Thousand insects of Japan* (Additam.) **4**: 743–962.

MATSUMURA, S. (1933) New species of Cymatophoridae of Japan and Formosa. *Insecta Matsumurana* **7**: 190–201.

MELL, R. (1942) Beiträge zur Fauna sinica XXIII. Über die Cymatophoridae von Kuangtung. *Archiv für Naturgeschichte* (N. F.) **11**: 293–303.

MOORE, F. (1888) Description of new genera and species of Heterocera Lepidoptera, collected by Rev. J. H. Hocking, chiefly in the Kangra District, N. W. Himalaya. *Proc. zool. soc. London,* **1888**: 390–412.

ROEPKE, W. (1944) Remarks on new or little known Indomalayan moths (Lepid. Heteroc.). XI. *Natuurhistorisch Maandblad* **33**: 65.

SWINHOE, C. (1894) New species of eastern Lepidoptera. *The Annals and Magazine of Natural History including Zoology, Botany and Geology, London* **14**(6): 429–443.

WARREN, W. (1915) Some new Oriental Cymatophoridae in the Tring Museum. *Novitates zoologicae* **22**: 154–159.

WILEMAN, A. E. (1911) New and unrecorded species of Lepidoptera Heterocera from Japan. *Trans. ent. soc. London* **1911**: 189–407.

WILEMAN, A. E. (1914) New species of Heterocera from Formosa. *Entomologist* **47**: 318–323.

YOSHIMOTO, H. (1983) Descriptions of a new genus and a new species of Thyatiridae from the Malay Peninsula (Lepidoptera). *Tinea* **11**: 155–159.

YOSHIMOTO, H. (1983): A Revision of the Genus Demopsestis and Its Three Related Genera, with Description of a New Species from Taiwan (Lepidoptera, Thyatiridae). *Tyo Ga* **34**(1): 1–20.

YOSHIMOTO, H. (1987) Notes on Mimopsestis Matsumura, 1921, and its allied new genus, with descriptions of three new species from Southeast Asia (Lepidoptera, Thyatiridae). *Tyo Ga* **38**(1): 39–53.

YOSHIMOTO, H. (1990) Takapsestis fascinata sp. n. from China (Lepidoptera, Thyatiridae). *Nota lepid.* **13**(4): 236–241.

YOSHIMOTO, H. (1992) Thyatiridae. *In* Haruta, T. (ed.): Moths of Nepal, Part I. *Tinea* **13**(suppl. 2): 47–49.

YOSHIMOTO, H. (1994) Thyatiridae. *In* Haruta, T. (ed.): Moths of Nepal, Part III. *Tinea* **14**(suppl. 1): 91–94.

YOSHIMOTO, H. (1996) Records of Thyatiridae from Thailand (Lepidoptera). *Tinea* **14**(4): 279–286.

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THE MEADOW AND STEPPE VIPERS OF EUROPE AND ASIA – THE VIPERA (ACRIDOPHAGA) URSINII COMPLEX

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The systematic position and validity of the currently recognised subspecies in the '*Vipera ursinii* s. l. complex' (=*Acridophaga*) are evaluated from phenetic and phylogenetic perspectives. The West Asian and European mountain populations have evolved independently. A picture emerges of one group of comparatively widespread lowland taxa and three different assemblages of mountainous taxa. The lowland group covers *rakosiensis*; *moldavica*, west and east *renardi*, and the mountain groups consist of:

– the European ones (Italian *ursinii*, French *ursinii, macrops* and *graeca*)
– the Transcaucasian and Turkish (*lotievi, eriwanensis, ebneri* and *anatolica*)
– the Transcaspian and Chinese ones (*tienshanica* ssp.n. and *parursinii* ssp. n.).

To the eastern group, the lowland 'Altai form of *renardi*' must be added. This is a taxon with "mountain morphology".

The various mountain populations ranging from France in the west to China in the east are characterised by a series of convergent adaptations (homoplasies). In addition, they are adapted to mountain and/or alpine habitats and environments.

1. Immunological and electrophoretical characteristics analysed with cladistic and phylogenetic methods support a north-south relationship between taxa (JOGER *et al.* 1992, NILSON *et al.* 1993).

2. Newer observations and records revealed that several traditionally used morphological character states used in phylogenetic discussions are reversals and convergences (e.g. 19 midbody scale rows).

3. A cladistic analysis of the revised morphology (2., above) results in a unanimous phylogeny consistent with the results of the molecular analyses (1., above).

From a cladistic point of view, the most derived group are the different mountain populations, a hypothesis based on cladistic phylogenetics, and supported by two alternative approaches: molecular and morphometric.

The following taxa are monophyletic and fulfil the criteria of the phylogenetic species concept: ((((*rakosiensis*) (Italian *ursinii*) (*macrops, graeca*)) (French *ursinii*) (*moldavica*)) (((*west-renardi*) (((*eriwanensis*) (*anatolica*) (*ebneri*)) (*lotievi*)))((*east-renardi*) ((*tienshanica*) (('Altai form of *renardi*') (*parursinii*)))))). Biochemical analyses support the major pattern in this picture with the difference of placing *moldavica* as a sister taxon to *macrops* and *graeca*.

We consider *renardi* as a good species, and consequently none of its descendant populations *anatolica, eriwanensis, ebneri, tienshanica*, the 'Altai form of *renardi*' and *parursinii* can be subspecies of *ursinii* s.str. To reflect the evolutionary history a nomenclature shift is performed. Earlier, several of the eastern taxa have been raised to species level, or are treated as such in the present work. The relationship of *Vipera darevskii* and *Vipera pontica* remains uncertain.

INTRODUCTION

The subspecific division of *Vipera ursinii* s. l., as well as the phylogenetic position of the species within *Vipera* s. l. have long been subject to disputes among taxonomists. The traditional view is a species with a highly fragmented distribution in Europe and West and Central Asia, often isolated on subalpine meadows, xeromontane meadows or grassy orobiomes on different mountain ridges. Some populations are situated geographically close on nearby mountain peaks, but still effectively isolated from each other by deep valleys, and seem to have been isolated in such a way for geologically long periods. Occasionally, there are greater morphological differences between nearby populations than between some very distant ones.

Low degree of morphological/genetic variation in populations inhabiting previously glacial regions have been observed in species of reptiles and amphibians. The loss of such variation has been hypothesised to be the result of genetic drift following colonisation from source populations surviving in glacial refuges (dispersal). Alternatively, the glaciation that occurred over a former range of *Vipera ursinii* s. l. may have fragmented populations into smaller demes with restricted gene flow (vicariance). This could result in removal of polymorphism through the enhanced effects of selection and/or genetic drift. The extension of forests might also have been an important factor in this case.

In evolutionary biology, the taxonomic division should reflect the phylogeny and the speciation process. When the range of a species is fragmented by vicarian or dispersal events, the different subpopulations are submitted to different selection. In "old" species, approaching extinction, the original, wide-spread population might have been fragmented into declining populations, which finally disappear. In such case, a taxonomic division does not reflect the evolutionary process.

Before one can evaluate the most accurate taxonomic pattern for *Vipera ursinii*, an important question must be addressed (NILSON & ANDRÉN 1987). Are the different isolated mountain populations of phylogenetically younger origin and thus reflecting the speciation process, or are these populations' old remnants of a once wider distribution and hence reflecting a process of 'natural' extinction?

Ten different subspecies have been recognised in the recent literature. Of these *Vipera ursinii ursinii* in Italy, *Vipera ursinii wettsteini* in France, *Vipera ursinii macrops* in Western Balkan peninsula, and *Vipera ursinii anatolica* in Southern Turkish Anatolia are all mountain taxa, and have 19 mid-body scalerows. *Vipera ursinii rakosiensis* also has 19 mid-body scalerows, but is a lowland inhabitant with a present occurrence in Hungary, formerly in Austria, and, according to

various sources Bulgaria (e.g. KRAMER 1961). It has up to recently had an occurrence in Romania (Cluj).

In the former Soviet Union and adjacent parts of Asia, taxa with 21 dorsal scale rows occur. Populations referred to *renardi* are found in Ukraine, Russia, Kazakhstan, Kirgizia and northern China. Populations referred to *Vipera ursinii eriwanensis* are found in the Armenian highlands and upland Western Azerbaijan of the former U.S.S.R, and adjacent parts of Turkey. Populations referred to *Vipera ursinii ebneri* are found in northern Iran and Southern Azerbaijan. Many authors agree totally or to some part with this subspecific pattern (e.g. KNOEPFFLER & SOCHUREK 1955, MERTENS & WERMUTH 1960, EISELT & BARAN 1970, OBST 1983, DELY & STOHL 1984, JOGER 1984, ENGELMAN *et al.* 1986). Others place the western mountain populations, i.e. *wettsteini*, *ursinii*, *macrops* and *anatolica* as a single taxon: *V. u. ursinii*, and *V. u. rakosiensis* as a related lowland subspecies. In concordance with this model, the eastern populations (with 21 dorsal scale rows) are classified either as *Vipera ursinii renardi* alone or as *V. u. renardi* and *Vipera u. ebneri* (or *V. u. eriwanensis*). The former is distributed in the northern lowland parts (mainly former USSR) and the latter in the southern mountain regions (eastern Turkey, Armenia, Western Azerbaijan, and northern Iran, meanwhile also including the populations in Kirgizia, eastern Kazakhstan and neighbouring China). This last view is based on the work of KRAMER (1961) and has been adopted by some authors (e.g. SAINT GIRONS 1978, 1980, BARON 1987). VOZENILEK (1979) goes further and includes also *rakosiensis* in *u. ursinii* s. str.

In addition, the Greek Mountain populations have been described as *Vipera ursinii graeca* (NILSON & ANDRÉN 1988) and the eastern Romanian ones as *Vipera ursinii moldavica* (NILSON *et al.* 1993). The related populations of the high Caucasus have been described as *Vipera lotievi* (NILSON *et al.* 1995).

The taxonomic history of this complex has partly been summarised by DELY and STOHL (1984). The taxonomic history for the complex in the Caucasus and Transcaucasus has to some part been reviewed and discussed by ORLOV and TUNIYEV (1986, 1990), and by NILSON *et al.* (1994, 1995). In recent times, our studies of this complex have led to the discovery of a more complicated taxonomy and phylogeny than could be detected from morphometric studies alone (JOGER *et al.* 1992, NILSON *et al.* 1993). This has led us to separate several of the *ursinii* taxa on the species level, including the discovery of new taxa.

This study is an attempt to reanalyse the morphology of the members of this complex, and to re-evaluate morphology as a tool in evolutionary systematics, compare it to biochemical studies performed simultaneously, and to phenetic and phylogenetic (cladistic) methods. We believe that a combined analysis with all these different methods could give a reliable image of the phylogenetic process.

Furthermore, we will discuss the species concept and taxonomic pattern from an ecological and a reproductive perspective. It must be stated here that we are advocates of a taxonomy that reflects the evolutionary history, as is the case with the evolutionary and phylogenetic species concepts. Both are emanating from the purpose to clarify the evolutionary history. We do not consider the biological species concept as accurate for allopatric populations, as it is based on a joint plesiomorphy: reproduction. However, in parapatric and sympatric natural situations reproductive isolation seems to be an excellent mechanism in the speciation process in vipers (NILSON 1998).

MATERIAL AND METHODS

Several localities with *Vipera ursinii* s. l. were visited during the years and the snakes were studied "in situ". Measurements were taken and the specimens afterwards were released at the place of capture. Habitat was examined and the habitat choice and demands for almost all taxa was recorded, in order to understand relationships, ecological niche, and phylogenetic patterns. During parts of the study, it was necessary to collect tissues and blood samples. In most cases, this could be done from captive specimens in Europe. For details, see Acknowledgement.

Altogether, more than 1000 preserved or live specimens of *Vipera ursinii* were measured in this study, representing all currently or formerly recognised subspecies as well as new ones. Most of the specimens used are from various museum collections. A very large collection of Austrian *Vipera ursinii rakosiensis* is deposited in the Naturhistorisches Museum Wien. It has not been feasible to examine all snakes in such a large sample from a single locality and in those cases, a suitable series was chosen (Table 1). However, it must be pointed out that from most localities only very small samples are available.

Morphology/phenetics

We also employ multivariate statistical techniques to compare characters and proportions simultaneously among taxa and populations.

For the morphological and multivariate analyses, 435 snakes from more than 70 localities within the *ursinii* complex have been examined more carefully (Table 2). For most of these specimens 46 morphological characters of scalation and colour pattern have been collected (Table 3). Statistics used when comparing taxa were one-way and 2-way ANOVA, with sex and locality, or sex and taxon, as the two independent variables. Principal component analyses (PCA) was also performed.

PCA is a procedure for data reduction to find structural relationships among specimens without *a priori* subdivision of the specimens into discrete groups. The aim is to reveal the patterns of geographic variation among all OTUs and construct new orthogonal axes, which are linear combinations of the original variables. PCA is first undertaken without any clear objective and then an attempt is being made to interpret the resultant data. The axes are constructed to maximally explain dispersion in the multivariate data set. Thus, often, a large proportion of variation in the original data can be parsimoniously explained by only a few components. The PCA used in this study was based on a correlation matrix of 15 most informative meristic characters for both males and females.

Table 1. The material used for detailed studies represents the currently recognized subspecies and is divided as follows

Taxa	N	
Italian *V. u. ursinii* (= *ursinii*)	33	
French *V. u. ursinii* (=*wettsteini*)	35	if not otherwise stated, pooled to *ursinii* s. str.
V. u. macrops	44	
V. u. graeca	14	
V. u. rakosiensis	62	
V. u. moldavica	43	
V. r. renardi	59	Here treated as two samples: east *renardi* and west *renardi*
V. r. tienshanica	19	This paper
V. r. parursinii	31	This paper
'Altai form of *V. renardi*	53	In prep.
V. anatolica	4	
V. eriwanensis	47	
V. ebneri	16	
V. lotievi	25	

Table 2. Specimens used in the statistical analyses, arranged into samples. Localities are mapped in Fig. 1. Unnumbered localities are not fully included in the analyses (Details of specimens examined are in the taxonomic section.)

Sample locality	Sample size		
	male	female	total
V. u. ursinii (highland populations)			
1. France, Mt. Ventoux	5	1	6
2. France, Mt. de Lure	4	12	16
3. France, Basses Alpes, Lac de Lignins	2	2	4
4. France, Basses Alpes, La Cassine	2	2	
5. France, Basses Alpes, Turriers		1	1
6. France, Basses Alpes, Mourre de Chanier		1	1
7. France, Alpes Maritimes, Plateau Coussul	1	4	5
8. Italy, Mt Sibillini Vettore	6	12	19
9. Italy, Mt. Velino		3	3
10. Italy, Gran Sasso	3	4	7
11. Italy, Abruzzo N. P.	1		1
12. Italy, Monti della Laga	1		1
Italy, NE Rome			2

Table 2 (continued)

Sample locality	Sample size		
	male	female	total
V. u. macrops (highland populations, except pop. 20)			
13. Bosnia-Herzegovina, Blejasnica Planina		1	1
14. Yugoslavia (Montenegro), Durmitor	1	1	2
15. Bosnia-Herzegovina, Korita	6	10	16
16. Bosnia-Herzegovina, Cemerno, Mt. Lebrsnik	4	3	7
17. Bosnia-Herzegovina, Baba Planina	9	5	14
18. Bosnia-Herzegovina, Troglav		1	1
19. Bosnia-Herzegovina, Lebroznik	1	1	2
20. Croatia, Krk			1
graeca (highland population)			
21. Greece, Pindos	9	5	14
V. u. rakosiensis (lowland populations)			
22. Austria, Laxenburg	1	4	5
23. Austria, Grammat-Neusiedl	6	3	9
24. Hungary, Ócsa, Soroksár	2	4	6
25. Hungary, Budapest, Pest County	1	7	8
26. Hungary, Dabas	9	12	21
27. Hungary, Kunpeszér	4	6	10
28. Hungary, Bugac		1	1
29. Bulgaria, Sofia (*moldavica*?)	1	1	2
V. u. moldavica (lowland populations)			
30. Bulgaria, Sumen	1	1	2
31. Romania, Valea lui David	8	8	16
32. Romania, Calarasi-Dorohoj	1		1
33. Romania, Romanesti/Ursaia	9	8	17
34. Romania, Carpathians, Mt. Rarau		1	1
35. Romania, Danube Delta, Bratul Sf. Gheorghe		3	3
36. Romania, Danube Delta, C. A. Rosetti	1	1	2
37. Romania, Danube Delta, Grindur Perisor		1	1
V. renardi (lowland and foothill populations)			
38. Ukraine, Ile Orlov	3	5	8
39. Ukraine, Dnjepr	9	4	13
40. Ukraine		1	1
41. Russia, Stalingrad, Saratov	4		4
Russia, Sarepta	1		1

Table 2 (continued)

Sample locality	Sample size		
	male	female	total
42. Russia, Kislowodsk, Pjatigorsk			3
43. Azerbaijan, Shemakha			1
'former Soviet Union'	1		1
44. Russia, Omsk, Tomsk	2	1	3
45. Kazakhstan	1		1
46. Kazakhstan, Sasykkol		1	1
47. Kazakhstan, Dzherzkazgan	5	5	10
48. Kazakhstan, Alma-Atinsk, Akterek, Dzambukski	3	2	5
49. Kazakhstan, Tarbagatai Mountains	2	5	7
V. r. tienshanica (highland populations)			
50. Kirgizia, Chinas (Tschinas)	3	1	4
51. Kazakhstan, Almaty, Varnoe	3	1	4
52. Kirgizia, river Tschu, N. Frunze (Bishkek)	3	1	4
53. China, Xinjiang ('E. Turkestan'), Yining (Kuldja)	2	1	3
54. China, Xinjiang, Yumin Xian	2	1	3
55. China, Xinjiang, Tacheng Xian (Qoqek)	1		1
V. r. parursinii (highland populations)			
56. China, Xinjiang, Xinyuan Xian (Künes)	3	2	5
57. China, Xinjiang, Nilka Xian	12	14	26
The 'Altai form of *V. renardi*' (lowland populations)			
58. China, Xinjiang, Hababe Xian (Kaba)	4	2	6
59. E. Kazakhstan, Altai Mountains, Talgir			15
60. E. Kazakhstan, Altai Mountains, Kuzchum, Slaviyanka			19
61. E. Kazakhstan, Saur Mountains			13
V. anatolica (highland populations)			
62. Turkey, Ciglikara	1	3	4
V. eriwanensis (highland populations)			
63. Armenia, berg Ara-Iler	11	6	17
64. Armenia, Yerevan-Sevan region	3	5	8
65. Turkey, Sarakamis, Asbua	7	4	11
66. Turkey, Kagizman, Günindi	4	3	7
67. Turkey, Kars, Arpacay	1	3	4
V. ebneri (highland populations)			
68. Iran, Elburz Mountains, Lar valley	7	8	15
Iran	1		1

Table 2 (continued)

Sample locality	Sample size		
	male	female	total
V. lotievi (highland populations)			
69. Russia, Caucasus, Ingushetia, Armhi	6	8	14
70. Russia, Caucasus, Checheno-Ingushetia, Stolovaya	4		4
71. Caucasus, Kabardino-Balkaria, Terskol		1	1
72. Caucasus, Mt. Bolskaya, Halipari		1	1
73. East Caucasus, Lagodechi		1	1
74. East Caucasus, Gunib, Mehetta	1	2	3
75. Caucasus, Elbrus		1	1
Total			488

In order to avoid one variable having an undue influence on the principle components, all variables were standardised to have means of zero and variances of one at the start of the analysis.

Further canonical variate analyses (CVA) was used. It is a technique for examining the interrelationships between a number of populations (*a priori* groups) simultaneously, with the end in view of representing the interrelationships graphically in only a few dimensions. The axes are constructed as to maximise between-group variance relative to the within-group variance. Thus, the canonical variates have greater discriminatory power than any single character.

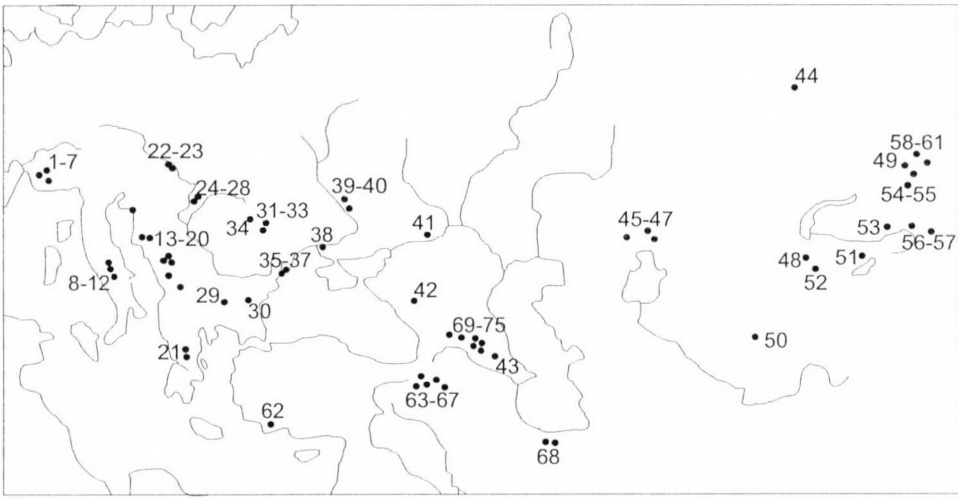


Fig. 1. Examined Museum material of the *ursinii* complex in Europe and Asia (o), numbered according to Table 2

Table 3. Morphological characters used

1	Sex
2	Total length
3	Relative tail length
4	Number of preventrals, defined as those gular scales anterior to ventrals that are broader than long
5	Number of ventrals, following the Dowling (1951) method
6	Number of subcaudals
7	Number of anterior dorsal scale rows, counted one head length posterior of head
8	Number of mid-body dorsal scale rows, counted at the exact middle of the body
9	Number of posterior dorsal scale rows, counted one head length anterior to anal
10	Ventral number for the reduction of dorsal scalerows from 21 to 19
11	The shape of the rostral, given as height/breadth
12	Number of apical plates in contact with rostral
13	Total number of plates in contact with rostral
14	Number of supralabials (right + left)
15	Number of sublabials (right + left)
16	Number of scales in the circumocular ring, counted as right and left sides together
17	Number of loreals (right + left)
18	Number of second chinshields, i.e. the number of scales in the transverse mental row posterior to the anterior chinshields and on each side incontact with the sublabials
19	Number of mentals, between the anterior chinshields and the preventrals
20	Number of canthals
21	Number of intercanthals + intersupraoculars, which are all scales
22	If parietals are divided/fragmented or not
23	If frontal is divided or not
24	Number of nasorostralia (right + left)
25	If nasalia is normal, divided or united with nasorostralia
26	Number of supralabials between rostral and level of eye (right + left)
27	Clear size difference between anterior and posterior supralabials or not
28	Head length, measured from posteriormost edge of parietals to tip of snout
29	Head breadth, measured at the level of the eyes
30	Horizontal eye diameter
31	Vertical eye diameter
32	Length of snout, measured from anterior border or eye to suture between nasorostralia and rostral
33	Distance between eye and lip
34	Upper preocular in contact with nasal or not
35	Lower preocular in contact with nasal or not

36 Number of windings in dorsal zigzag band
37 Ground colour
38 Ventral colour, which may be dark or light
39 Colour of dorsal pattern
40 Shape of the neck pattern
41 Labial-pattern, which may consist of dark labial sutures or not
42 Shape of dorsal side of head, which may be concave or flat
43 Presence of lateral or dorsolateral body blotches or not
44 Colour of third last maxillar plate
45 Presence or absence of frontal spot
46 Size of intersquamose area

Table 4. Methods used in this and additional studies for resolving the phylogeny of the *Vipera ursinii* s. l. complex. Abbreviation: 1 = JOGER *et al.* 1992, NILSON *et al.* 1993, 2 = this paper, 3 = NILSON *et al.* 1994, 1995, 4 = NILSON & ANDRÉN 1997, 5 = JOGER *et al.* 1992, NILSON *et al.* 1993, 6 = this paper

	Methods					
	1	2	3	4	5	6
	Albumin Immunology	Morphometry Cladistics	Allozyme Electrophoresis	Reproduction	Albumin Electrophoresis	Morphometry Phenetics
V. renardi	+	+	+	+	+	+
V. eriwanensis	+	+	+	+		+
V. u. ursinii (Italy)	+	+		+	+	+
V. u. ursinii (France)	+	+		+	+	+
V. u. macrops	+	+			+	+
V. u. rakosiensis	+	+			+	+
V. u. graeca	+	+			+	+
V. u. moldavica	+	+			+	+
V. anatolica	+	+			+	+
V. ebneri		+				+
V. r. parursinii		+				+
V. r. tienshanica		+				+
V. lotievi		+	+			+
'Altai form of *V. renardi*'		+				+

In addition, the jack-knifed classification procedure based on a matrix of Mahalanobis distances was used to evaluate the group membership of all the specimens to the group with which they shared the greatest morphological similarity.

For the analysis of intra- and interpopulational morphological variation (phenetic analysis) the samples were divided into a large number of subsamples depending on available material (see Tables 1–2, and Fig. 1). For this part of the work, a geographical division was followed, with less consideration of the traditional subspecific pattern. Thus besides an analysis of morphological variation also a pattern confirming or rejecting the present taxonomic pattern could be achieved. However, also a pattern that could be supported or rejected by the parallel biochemical studies could be achieved. In this way, it is possible to estimate the occurrence of convergent or parallel evolution. These results were compared with parallel analyses performed elsewhere (Table 4).

Character coding and phylogenetic analyses

Characters were coded into discreet states for phylogenetic analyses (PAUP procedure). A main object in the cladistic analysis is to select characters that have evolved in a unique way and reflect the evolutionary history.

It can be suspected (see below) that a number of characters are homoplasies and reflecting adaptations to similar habitats or niches rather than to a similar evolutionary history and phylogeny. Certain morphological characters in snakes seem to vary due to external influences rather than being passed on by heredity. Temperatures during the embryogenesis can be one such influence (e.g. FOX *et al.* 1961, VINEGAR 1973, PETERSON *et al.* 1993, BRODIE III & GARLAND 1993). Thus, there is a possibility that characters may change in one direction in all mountain and subalpine populations due to cold climate and in an opposite direction in all lowland populations due to warm climate. Such characters may be of no phylogenetic value due to phenotypic expression. Some characters vary in a similar way in all alpine populations and in an opposite way in all nearby lowland populations throughout the range of *Vipera ursinii* s. l. A few such characters have been omitted, as they may reflect convergence (see 'Analyses of morphological characters', below).

Used morphological characters are listed in Tables 43–45. The characters were qualitatively coded into discrete states for analysis in the two computer programs PAUP (Phylogenetic Analysis Using Parsimony, version 3.0; SWOFFORD 1991) and MacClade (Analysis of phylogeny and character evolution, version 3.0; MADDISON & MADDISON 1992). The 23 morphological characters were coded into ordered binary states. The branch-and-bound algorithm in PAUP was employed to obtain the most parsimonious cladogram(s). This exact search procedure saves the shortest tree(s), e.g. minimising the amount of reversals, parallelisms and convergence, of all possible fully dichotomous trees compared for the 12 terminal taxa.

Biochemistry

Electrophoretic analyses of serum albumins, and studies in immunology were made simultaneously (JOGER *et al.* 1992, HERRMANN *et al.* 1992, NILSON *et al.* 1993) as well as studies of isozyme biochemistry of *ursinii* taxa (NILSON *et al.* 1994, 1995). The results from these papers are further discussed in the present paper.

Ecological comparisons

Habitat and altitude analysis

France. Mt. de Lure in the Basses Alps in France was visited in September 1974 and in June 1990. The Coussol Plateau was visited in June 1990 and a few specimens of *ursinii* were spotted and

photographed in the field. The habitats were documented. Additional information about habitats in France was submitted by HERBERT BILLING and HANS NEUMEIER in Zürich.

Italy. The Italian population of *ursinii* was the only one that we could not visited during this study. Information about habitats in Italy was submitted by HANS TRIET, Bern, HERBERT BILLING and HANS NEUMEIER in Zürich, and by BRIAN GROOMBRIDGE, Cambridge.

Former Yugoslavia. Bosnia-Herzegovina was visited in June 1987, where *macrops* habitat could be studied at several places. This taxon was observed at the type locality (Korita).

Greece. The Pindos Mountains in Greece were visited 1986 and the habitat was examined. This visit led to our description of *V. u. graeca* (NILSON & ANDRÉN 1988).

Austria and Hungary. Lower Austria and Hungary have been visited a number of times between 1985 and 1998 for conservation work. As members of the SEH Conservation Committee, we have evaluated the past and present situation for *rakosiensis* (CORBETT 1986*a*, *b*, 1989), and Hungarian specimens were examined and photographed in the field at four different localities.

Romania. In July 1988, we were able to stay for some days in the Jasi region of Romanian Moldavia, and on Mt. Rarau in the northern Carpathians. Thereby we were able to visit the habitats of the Moldavian *ursinii*. This work led to our description of *moldavica* (NILSON *et al.* 1993).

Russia. In July 1990 and June 1992 we visited different parts of the Caucasus mountain range and were able to study some habitats of lowland and mountain populations of *ursinii* s. l. This work led to our description of *lotievi* (NILSON *et al.* 1995).

Turkey. Ciglicara in South Turkey, which is the type locality for *Vipera ursinii anatolica*, was visited in 1973, 1981 and 1982 for other studies, and the *anatolica* habitat was examined.

Armenian plateau. In east Turkey the Sarakamis region of Kars province was visited in 1986, the Kagizman region in 1988, and the Cildir region, where the habitat for *eriwanensis* was studied, in 1989. In 1992 different parts of Armenia were visited and a number of localities and specimens of *eriwanensis* were seen. Habitats and specimens were also observed at the border area between Armenia and Azerbaijan.

Iran. The upper Lar valley in the Elburs Mountains in northern Iran was visited in 1973 and 1976, and the habitat for *ebneri* was studied. Live specimens were seen at the Razi Serum Institute in Hessarak/Teheran 1973.

Kazakhstan. Fieldwork was performed in the Tien Shan Mountains south of Almaty and on the steppe region northwest of Dzungarsky Alatau mountain range in September 1996. Further field work was performed in the Altai Mountains in July 1997 and June 1999, on the steppe south of the Altai Mountains in 1998 and 1999, in the Tarbagatay Mountains in September 1998, and in the Saur Mountains in July 1999.

Reproductive comparisons

Reproductive studies of this group among other viperin snakes used here have been presented elsewhere (see NILSON & ANDRÉN 1989, 1997, and references therein), but the information is to a certain extent re-evaluated here. In addition, available literature information and field observations have been used.

Museum abbreviations

BMNH – British Museum (Natural History), London; CAS – California Academy of Sciences, San Francisco; CNR – Caucasian Nature Biosphere Reserve, Collection of Boris Tuniyev at You Box Groove, Sochi; CIB – Chengdu Institute of Biology, Chengdu; GNM – Göteborgs Naturhistoriska Museum, Göteborg; HNHM – Hungarian Natural History Museum, Budapest; MNHN –

Museum National d'Histoire Naturelle, Paris; MHNG – Museum d'Histoire Naturelle, Genève; MINJ – Muzeul de Istoire Naturala, Jasi; MTKD – Staatliches Museum für Naturkunde, Dresden; MZF – Museo Zoologico de "La Specola", Florence; NMW – Naturhistorisches Museum, Wien; NRS – Naturhistoriska Riksmuseet, Stockholm; UMMZ – University of Michigan, Museum of Zoology, Ann Arbor; ZIG – Department of Zoology, Göteborg University, Göteborg (authors' collection, which later will be incorporated in GNM); ZIS – Zoological Institute, Bulgarian Academy of Sciences, Sofia; ZISP – Zoological Institute, Academy of Sciences, St. Petersburg; ZMK – Zoologisk Museum, Copenhagen.

RESULTS

Phenetics

Analysis of morphological characters

Most measured characteristics are discussed here, except some that have no direct informative value, show little or no variation or were considered as being too subjective (numbers correspond to Table 3). However, some of these are included elsewhere in this paper. For several characters, different presentations are made for the sexes, in order to express eventually present sexual dimorphism.

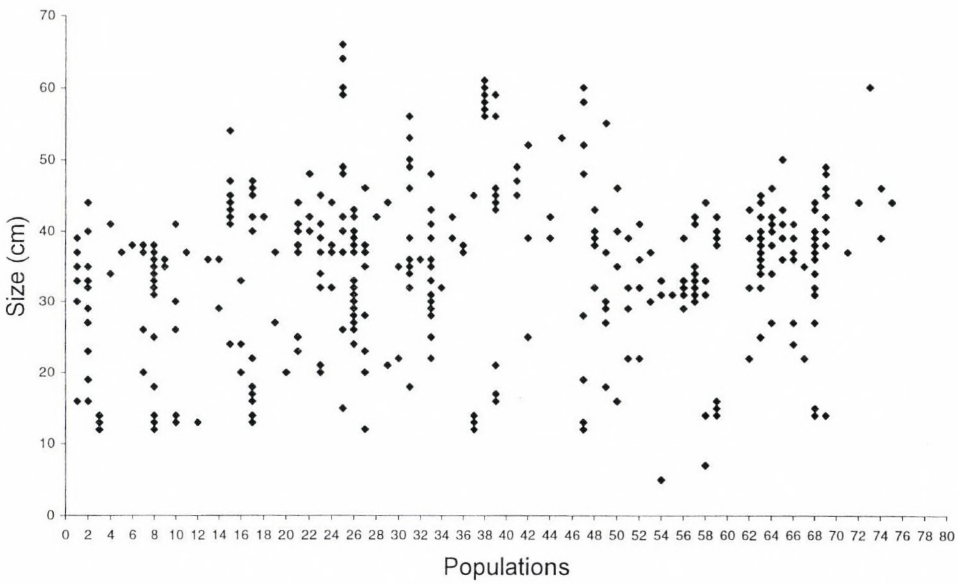


Fig. 2. Total length (head, body and tail) of all measured specimens in the investigated populations. Population numbers as in Table 2 and Fig. 1

Total length (Fig. 2). The members of the *ursinii* complex are rather small snakes with maximum lengths normally below half a meter. Of the maximum length of the measured specimens of the different taxa, *parursinii* is the smallest, with the largest specimen of 41.5 cm. Nevertheless, *graeca*, *ursinii*, and *ebneri* all have their maximum size between 43 and 44 cm. Maximum for *anatolica* is 43.0, however, in this case only four individuals were available.

Maximum for *tienshanica* 45.7, for *lotievi* 48.7 and for *eriwanensis* 50.1. Of the different mountain taxa *macrops* is the biggest and can reach sizes of 53.6 cm. The three lowland taxa are all bigger and in our material *moldavica* reaches 55.6, *renardi* 60.7, and *rakosiensis* attain 66.0 cm. The largest *rakosiensis* originates from the close surroundings of Budapest. The sample of the largest *renardi* specimens comes from the island Orlov in the Black Sea. Kotenko (1989) gives 70 cm as the maximum for that population.

Table 5. Number of preventrals in males

Taxa	N	Mean±S.E	Range
1. *V. u. rakosiensis*	23	2.09±0.14	1–3
2. *V. u. ursinii*			
3. *V. u. ursinii* (Italy)	11	1.55±0.25	0–3
4. *V. u. ursinii* (France)	12	1.42±0.23	0–3
5. *V. u. moldavica*	20	1.56±0.21	0–3
6. *V. u. macrops*	21	1.86±0.15	1–4
7. *V. u. graeca*	8	1.50±0.19	1–2
8. *V. anatolica**			
9. *V. eriwanensis*	26	1.92±0.14	1–3
10. *V. ebneri*	8	2.00±0.19	1–3
11. *V. lotievi*	6	2.50±0.22	2–3
12. *V. r. renardi***	31	2.16±0.11	1–3
13. *V. r. renardi* (west)	18	1.54±0.36	1–3
14. *V. r. renardi* (east)	13	2.15±0.15	1–3
15. *V. r. renardi* taxon (Altai)	5	2.20±0.20	2–3
16. *V. r. tienshanica*	15	2.40±0.18	1–4
17. *V. r. parursinii*	15	2.33±0.15	1–3

* In this and the following tables concerning males, *anatolica* is not included as only a single male was available

** In this and the following tables the *renardi* sample (12) is the 'traditional' *renardi* (Russian, Ukrainian and Kazakh populations), but excluding the Altai populations (15) and *tienshanica* (16)

Table 6. Number of preventrals in females

Taxa	N	Mean±S.E.	Range
1. *V. u. rakosiensis*	38	1.89±0.16	0–6
2. *V. u. ursinii*			
3. *V. u. ursinii* (Italy)	18	1.33±0.21	0–3
4. *V. u. ursinii* (France)	23	1.78±0.17	0–3
5. *V. u. moldavica*	23	2.04±0.15	1–3
6. *V. u. macrops*	20	2.00±0.19	1–4
7. *V. u. graeca*	5	1.60±0.25	1–2
8. *V. anatolica*	4	2.00±0.41	1–3
9. *V. eriwanensis*	21	2.09±0.14	1–3
10. *V. ebneri*	8	1.75±0.13	1–3
11. *V. lotievi*	12	2.33±0.14	2–3
12. *V. r. renardi*	22	2.32±0.13	1–3
13. *V. r. renardi* (west)	10	2.50±0.21	1–3
14. *V. r. renardi* (east)	12	2.16±0.16	1–3
15. *V. renardi* taxon (Altai)	6	2.16±0.17	2–3
16. *V. r. tienshanica*	4	1.75±0.48	1–3
17. *V. r. parursinii*	15	2.20±0.18	1–3

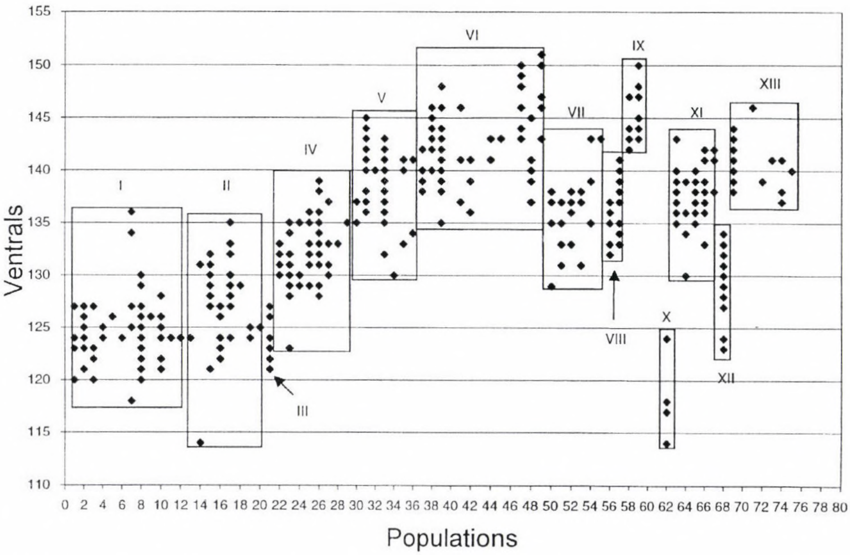


Fig. 3. Number of ventral scales in the investigated populations. Population numbers as in Table 2 and Fig. 1. Roman numbers indicating taxonomic divisions (I=*ursinii*; II=*macrops*; III=*graeca*; IV=*rakosiensis*; V=*moldavica*; VI=*renardi*; VII=*tienshanica;* VIII=*parursinii*; IX= *renardi* taxon (Altai form); X= *anatolica*; XI= *eriwanensis*; XII= *ebneri;* XIII= *lotievi*)

Table 7. Number of ventrals in males. Given as mean±S.E., range, and tested for differences in ventrals with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S. E.	Range	P<0.05
1. *V. u. rakosiensis*	23	131.13±0.66	(123) 128–136	3–7, 9, 11–12, 15
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	122.58±0.70	118–127	1, 5, 9, 11–12, 15–17
4. *V. u. ursinii* (Italy)	11	122.91±0.56	120–126	1, 5, 9, 11–12, 15–17
5. *V. u. moldavica*	20	138.00±0.65	134–144	1–4, 6–7, 10, 12, 15
6. *V. u. macrops*	21	126.14±0.90	(114)121–133	1, 5, 9, 11–12, 15–17
7. *V. u. graeca*	8	123.00±0.42	121–124	1, 5, 9, 11–12, 15–17
8. *V. anatolica*				
9. *V. eriwanensis*	26	136.39±0.41	(130) 133–143	1–4, 6–7, 10, 12, 15
10. *V. ebneri*	8	128.50±1.30	123–133	5, 9, 11–12, 15
11. *V. lotievi*	6	140.50±0.76	138–143	1–4, 6–7, 10, 17
12. *V. r. renardi*	31	141.71±0.58	135–148	1–7, 9–10, 16–17
13. *V. r. renardi* (west)	18	140.50±0.72	135–146	
14. *V. r. renardi* (east)	13	143.38±0.72	137–148	
15. *V. r. renardi* taxon (Altai)	5	144.80±0.66	143–147	1–7, 9–10, 16–17
16. *V. r. tienshanica*	15	135.67±1.01	129–143	3–4, 6–7, 12, 15
17. *V. r. parursinii*	15	133.93±0.30	132–137	3–4, 6–7, 11–12, 15

Number of preventrals (Tables 5–6). The number of preventrals approaches two in all taxa with the lowest value of around 1.5, or slightly higher in *graeca* and *ursinii*. *Graeca* is also characterised by pronounced reductions in several different scale characteristics. Italian female *ursinii* have by far the lowest values in this character. The highest values are found in male *lotievi* and female *renardi* (X=2.50). The largest span, from zero to six, can be seen in female *rakosiensis*. No statistical differences between taxa were found (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison).

Number of ventrals (Tables 7–8, Fig. 3). There is an increase in number of ventrals with increase in size between different populations. In addition, in the lowland taxa there is an increase towards the east. For both sexes in lowland populations, mean values are lowest for *rakosiensis*, higher for *moldavica*, and reaches top values for *renardi*. In the Middle East Mountains, there is an increase towards the northwest, with lowest values for *ebneri*, higher for *eriwanensis*, and highest for *lotievi*. The lowest values are found in single specimens of *anatolica* and *macrops* with 114 ventrals. The highest value (151) is found in a *renardi* specimen

Table 8. Number of ventrals in females. Given as mean±S.E., range, and tested for differences in ventrals with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S. E.	Range	P>0.05
1. *V. u. rakosiensis*	38	133.31±0.41	129–139	3–9, 11–12, 15, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	126.34±0.64	122–134 (136)	1, 5, 8–9, 11–12, 15–17
4. *V. u. ursinii* (Italy)	18	125.66±0.62	120–130	1, 5, 9, 11–12, 15–17
5. *V. u. moldavica*	23	139.78±0.70	130–145	1–4, 6–8, 10, 12, 15
6. *V. u. macrops*	20	128.65±0.69	122–135	1, 5, 8–9, 11–12, 15–17
7. *V. u. graeca*	5	125.40±0.81	123–127	1, 5, 9, 11–12, 15–17
8. *V. anatolica*	4	118.25±0.10	114–124	1–3, 5–6, 9–12, 15–17
9. *V. eriwanensis*	21	138.52±0.57	134–143	1–4, 6–8, 10, 12, 15
10. *V. ebneri*	8	131.25±0.65	129–134	5, 8–9, 11–12, 15, 17
11. *V. lotievi*	12	141.16±0.82	137–146	1–4, 6–8, 10
12. *V. r. renardi*	24	144.92±0.74	140–151	1–4, 6–10, 12, 17
13. *V. r. renardi* (west)	11	143.18±0.69	140–148	
14. *V. r. renardi* (east)	13	146.38±1.08	140–151	
15. *V. renardi* taxon (Altai)	6	147.66±0.92	145–150	1–10, 16–17
16. *V. r. tienshanica*	4	137.50±0.29	137–138	3–4, 6–8,15
17. *V. r. parursinii*	15	137.60±0.46	134–141	1–4, 6–8, 10, 12, 15

from Tarbagatai, Kazakhstan (east *renardi*), and in specimens of the 'Altai form of *renardi*' (no. 15). There is a clear sexual dimorphism in this character. Throughout all the taxa listed in the Tables 7 and 8, females have higher ventral counts than corresponding males.

ANOVA pairwise comparisons gave statistical differences between several taxa. Several related taxa can be separated on this character. Amongst others, significant differences can be seen between *renardi* and *eriwanensis,* between *renardi* and *ebneri*, between *renardi* and *parursini,* and between male *renardi* and male *tienshanica*. In addition, the 'Altai form of *renardi*' is significantly separated from the parapatric *tienshanica* and *parursinii. Ebneri* is significantly separated from *eriwanensis* and *lotievi*. *Rakosiensis* differs from all other European taxa, except female *lotievi,* etc.

Number of subcaudals (Table 9). This character expresses clear sexual dimorphism. All males have more subcaudals than females, but for certain taxa the males can have equal numbers or even fewer subcaudals than females of other taxa. This phenomenon is most pronounced in *graeca*, where females have only 19.4 subcaudal pairs, and males only 24.2, as mean values. This is also the most di-

Table 9. Number of subcaudals for each sex, given as mean±S.E., range, and tested for differences with other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	Males				Females		
	N	X± S.E.	Range	P≤0.05	N	X±S.E.	Range
1. *V. u. rakosiensis*	25	33.1±0.4	30–37	7	37	25.2±0.2	23–28
2. *V. u. ursinii*	23	31.1±0.3	27–35		41	24.5±0.3	20–32
3. *V. u. ursinii* (France)	11	30.6±0.6	28–35	5, 7 9, 12	22	24.5±0.3	22–27
4. *V. u. ursinii* (Italy)	11	31.3±0.4	27–32	5, 7	18	24.4±0.6	20–32
5. *V. u. moldavica*	21	35.9±0.5	32–41	3,4,6,7,10	23	26.9±0.4	23–32
6. *V. u. macrops*	22	32.0±0.4	29–35	5, 7	22	25.1±0.5	20–30
7. *V. u. graeca*	9	24.2±0.8	20–27	1,3–6,9–12,15–17	5	19.4±0.5	18–21
8. *V. anatolica*	*	–			4	21.3±0.9	19–23
9. *V. eriwanensis*	25	35.0±0.4	32–39	3, 7, 10	21	26.7±0.4	23–30
10. *V. ebneri*	8	30.4±1.4	23–34	5, 7, 9, 12	8	23.4±0.7	19–25
11. *V. lotievi*	6	35.2±1.4	33–38	7	12	25.6±0.5	23–27
12. *V. r. renardi*	30	34.8±0.4	28–38	3, 7, 10	24	27.1±0.3	24–29
13. *V. r. renardi* (west)	17	34.9±0.5	31–38		11	26.8±0.4	24–29
14. *V. r. renardi* (east)	21	34.3±0.5	28–38		14	27.5±0.5	24–30
15. *V. renardi* taxon (Altai)	5	36.0±0.9	33–35	7	6	27.3±0.5	26–28
16. *V. r. tienshanica*	15	34.4±0.7	28–38	7	4	27.8±0.5	27–29
17. *V. r. parursinii*	15**	32.7±0.3	32–35	7	15	25.7±0.5	23–30

* *V. anatolica* is not included as only a single male was available

** One male with abnormal tail and only 23 subcaudals was not included

vergent taxon, and statistically different from almost all other taxa in this character. The highest mean value for females (X=27.8) is found in the eastern mountain taxon, *tienshanica*, where males have 35.0. Highest values in males are found in *moldavica* (X=35.9) and in the 'Altai form of *renardi*' (X=36.0). Short tailed taxa with few subcaudals are *anatolica* and *ebneri*.

Number of anterior dorsal scale rows (Tables 10–11). Specimens and populations are characterised by either 19 or 21 dorsal scale rows on the neck depending on the level at which scale reduction takes place. This is discussed in more detail under character 10 below. The variation within the complex is statistically significant between several taxa (Tables 10–11), but shows no sexual dimorphism.

Number of mid-body dorsal scale rows (Tables 12–13). Similar as for character 7 with specimens and populations characterised by either 19 or 21 dorsal scale rows on neck, depending on at what level the scale reduction takes place.

Table 10. Number of dorsal scale rows on neck, one head length posterior of head in males. Given as mean±S.E., and range, and tested for differences in number of anterior scale rows with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	20.52±0.23	19–23	3, 4, 6, 7, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	19.33±0.23	19–21	1, 9, 10–12, 15,16
4. *V. u. ursinii* (Italy)	11	19.00±0.00	19	1, 9, 10–12, 15,16
5. *V. u. moldavica*	20	20.10±0.27	17–21	6, 9, 12
6. *V. u. macrops*	21	19.00±0.00	19	1, 5, 7, 9–12, 15, 16
7. *V. u. graeca*	8	19.00±0.19	18–20	1, 6, 9–11, 15, 16
8. *V. anatolica*				
9. *V. eriwanensis*	26	21.03±0.04	21–22	3–7, 17
10. *V. ebneri*	8	21.00±0.00	21	3, 4, 6, 7, 17
11. *V. lotievi*	6	21.00±0.00	21	3, 4, 6, 7, 17
12. *V. r. renardi*	31	21.25±0.11	21–23	3–6, 17
13.*V.* 'west-*renardi*'	18	21.15± 0.12	21–23	
14.*V.* 'east-*renardi*'	13	21.00± 0.00	21	
15. *V. renardi* taxon (Altai)	5	21.00±0.00	21	3, 4, 6, 7, 17
16. *V. r. tienshanica*	15	21.00±0.00	21	3, 4, 6, 7, 17
17. *V. r. parursinii*	15	19.06±0.07	19–20	1, 9–12, 15, 16

This is discussed in more detail under point 10 below. The variation within the complex is statistically significant between several taxa, but it shows no sexual dimorphism.

Number of posterior dorsal scale rows (Tables 14–15). Specimens and populations normally have 17 scale rows anterior to the anal. The group consisting of *moldavica*, *macrops*, and *graeca* differs from the rest by having less (X=16.35 in male *moldavica*, 15.57 in male *macrops*, 15.00 in male *graeca*; and 16.78 in female *moldavica*, 16.70 in female *macrops* and 15.14 in female *graeca*). In this character male *macrops*, and most of all *graeca* differ significantly from almost all other taxa. They also show the greatest range of variation within the local populations in this character (range of five or six rows, compared to a range of one to three rows in the other taxa).

In addition, Italian *ursinii*, and *anatolica* show tendencies in the same direction.

The variation within the complex is statistically significant between some taxa (see Tables 14 and 15).

Table 11. Number of dorsal scale rows on neck, one head length posterior of head in females. Given as mean±S.E., and range, and tested for differences in number of anterior scale rows with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	20.39±0.16	19–22	4, 6, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	19.56±0.19	19–21	9–12
4. *V. u. ursinii* (Italy)	18	19.00±0.00	19	1, 5, 9–12, 15, 16
5. *V. u. moldavica*	23	20.26±0.30	19–21	4, 6
6. *V. u. macrops*	20	19.10±0.10	19–21	1, 5, 9–12, 15, 16
7. *V. u. graeca*	5	19.00±0.00	19	9–12
8. *V. anatolica*	4	19.75±0.95	17–21	
9. *V. eriwanensis*	21	21.09±0.10	21–23	3, 4, 6, 7, 17
10. *V. ebneri*	8	21.00±0.00	21	3, 4, 6, 7, 17
11. *V. lotievi*	12	21.00±0.00	21	3, 4, 6, 7, 17
12. *V. r. renardi*	24	21.26±0.13	21–23	3, 4, 6, 7, 17
13. *V. r.* 'west-*renardi*'	11	21.54± 0.24	21–23	
14. *V. r.* 'east-*renardi*'	13	21.08± 0.07	21–22	
15. *V. renardi* taxon (Altai)	6	21.00±0.00	21	4, 6
16. *V. r. tienshanica*	4	21.00±0.00	21	4, 6, (17)
17. *V. r. parursinii*	15	19.46±0.22	19–21	1, 9–12, (16)

Dorsal scalerow reduction (Tables 16–17, Figs 4–7). The level of dorsal scale row reduction from 21 to 19 dorsal scale rows has an inter- and intra-populational variation that is more or less pronounced. Generally, the lowland populations, which normally consist of larger specimens, have a posterior reduction as opposed to mountain populations. However, this general rule is not constant. Especially eastern (Asian) mountain populations have a more posterior scale reduction, similar to the lowland taxa. Furthermore, some mountain taxa, such as *macrops*, can be comparatively larger, but never the less have an anterior scale reduction. There is also a lesser degree of variation within the different mountain and lowland taxa, respectively, which indicates that this character is not purely phenotypic or convergent adaptation due to environmental conditions.

The European and some Chinese mountain populations have the reduction very early on neck (in level between the 2nd and 27th ventrals; mean between 5.3 and 8.3 (Fig. 5), equal to a level between 4 and 8% of the ventrals).

In both the two European lowland subspecies, *rakosiensis* and *moldavica*, this reduction spans over a wide range, from ventral level 2 to 106. Most *renardi*

Table 12. Number of midbody dorsal scale rows in males. Given as mean±S.E., and range, and tested for differences in midbody scale rows with males of other taxa taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	19.26±0.14	19–21	9–12,15, 16
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	19.00±0.00	19	9–12,15, 16
4. *V. u. ursinii* (Italy)	11	19.00±0.00	19	9–12,15, 16
5. *V. u. moldavica*	20	19.20±0.20	17–21	9–12,15, 16
6. *V. u. macrops*	21	19.00±0.00	19	9–12,15, 16
7. *V. u. graeca*	8	18.62±0.26	17–19	9–12,15, 16
8. *V. anatolica*				
9. *V. eriwanensis*	26	21.03±0.04	21–22	1, 3–7, 17
10. *V. ebneri*	8	20.75±0.25	19–21	1, 3–7, 17
11. *V. lotievi*	6	20.83±0.17	20–21	1, 3–7, 17
12. *V. r. renardi*	31	20.87±0.07	19–21	1, 3–7, 17
13. *V.* 'west-*renardi*'	18	20.94± 0.05	20–21	
14. *V.* 'east-*renardi*'	13	20.85± 0.15	19–21	
15. *V. renardi* taxon (Altai)	5	20.80±0.20	20–21	1, 3–7, 17
16. *V. r. tienshanica*	15	20.60±0.18	19–21	1, 3–7, 17
17. *V. r. parursinii*	15	19.06±0.07	19–20	9–12, 15,16

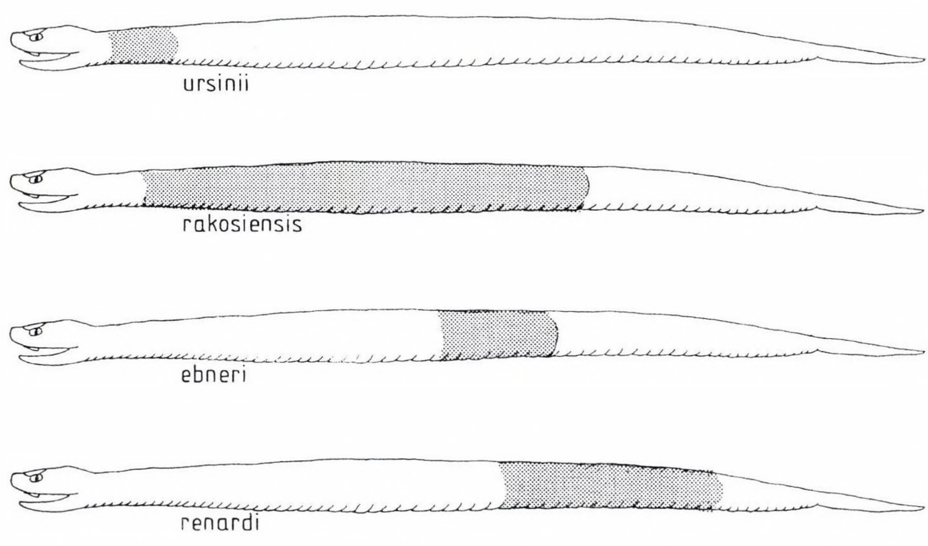


Fig. 4. Region for dorsal scale row reduction from 21 to 19 rows (SRL) (shadowed) in some of the investigated taxa

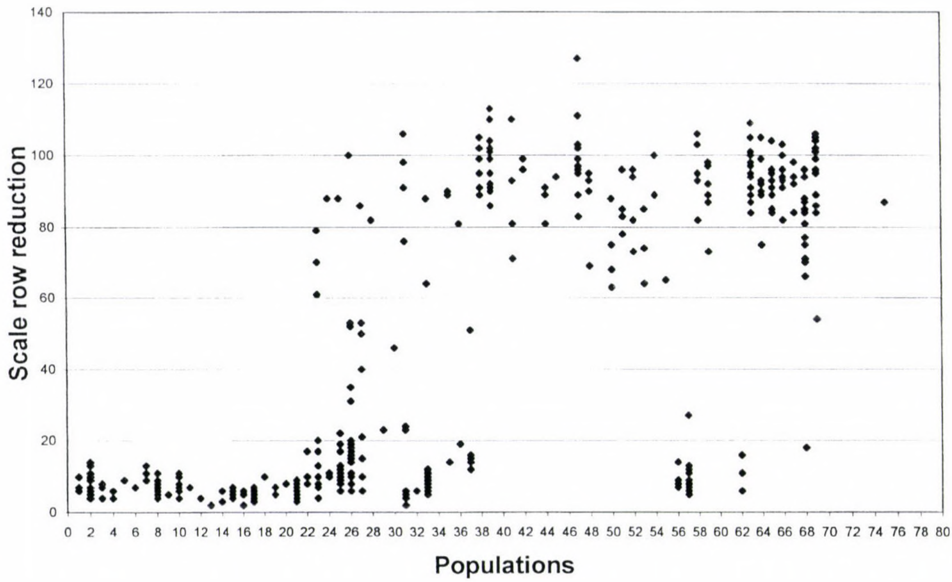


Fig. 5. Ventral scale number at the dorsal scale row reduction level (SRL), from 21 to 19 rows, in the investigated populations. Population numbers as in Table 2 and Fig. 1

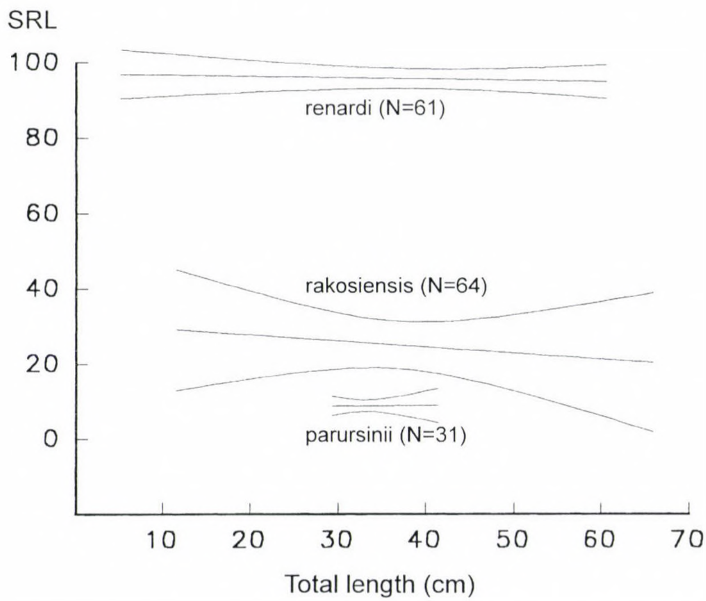


Fig. 6. Regression lines with 95% confidence intervals for level of dorsal scale row reduction (SRL) in *renardi*, *rakosiensis* and *parursinii* of different sizes. The scale row reduction is from 21 to 19 rows and plotted against corresponding ventral plate numbers

have the reduction on the posterior part of the body, between ventral 81 and 113, although single specimens can have an earlier reduction.

One specimen from Saratov, Russia, had a reduction at the level of 71st ventral. The specimen with the most posterior reduction level (at ventral 127) was a juvenile specimen of *renardi* from Dzherzkazgan, Kazakhstan, with a size of 12.6 cm. In general, there does not seem to be any positive correlation with size and level of reduction (Fig. 6).

However, a diverging pattern can be seen in *moldavica* (Fig. 7), where there seems to be a positive correlation with scale reduction level and size in those specimens that show a tendency towards having 21 dorsal scale rows. This pattern persists both in the Moldavian and in the Danube Delta samples independently, as well as in the two populations at Valea lui David and Romanesti in Romanian Moldavia (Fig. 7).

Most mountain populations in Asia have a posterior reduction similar to the lowland taxa. However, *Vipera anatolica* has an early reduction although somewhat delayed compared to the European mountain populations (between the 6th

Table 13. Number of midbody dorsal scale rows in females. Given as mean± S.E., and range, and tested for differences in midbody scale rows with females of other taxa taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u.rakosiensis*	38	19.23±0.10	19–21	9–16
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	18.95±0.04	18–19	9–16
4. *V. u. ursinii* (Italy)	18	19.00±0.00	19	9–16
5. *V. u. moldavica*	23	19.47±0.22	17–21	9–16
6. *V. u. macrops*	20	19.10±0.10	19–21	9–16
7. *V. u. graeca*	5	19.00±0.00	19	9–16
8. *V. anatolica*	3	19.00±0.00	19	9–16
9. *V. eriwanensis*	21	21.00±0.00	21	1–8,17
10. *V. ebneri*	8	20.75±0.25	19–21	1–8,17
11. *V. lotievi*	12	20.83±0.14	19–22	1–8,17
12. *V. renardi*	24	21.04±0.04	21–22	1–8,17
13. *V.* 'west-*renardi*'	11	21.00±0.00	21	
14. *V.* 'east-*renardi*'	13	21.08±0.07	21–22	
15. *V. renardi* taxon (Altai)	6	20.83±0.17	20–21	1–8,17
16. *V. r. tienshanica*	4	21.00±0.00	21	1–8,17
17. *V. r. parursinii*	15	19.02±0.15	19–21	9–16

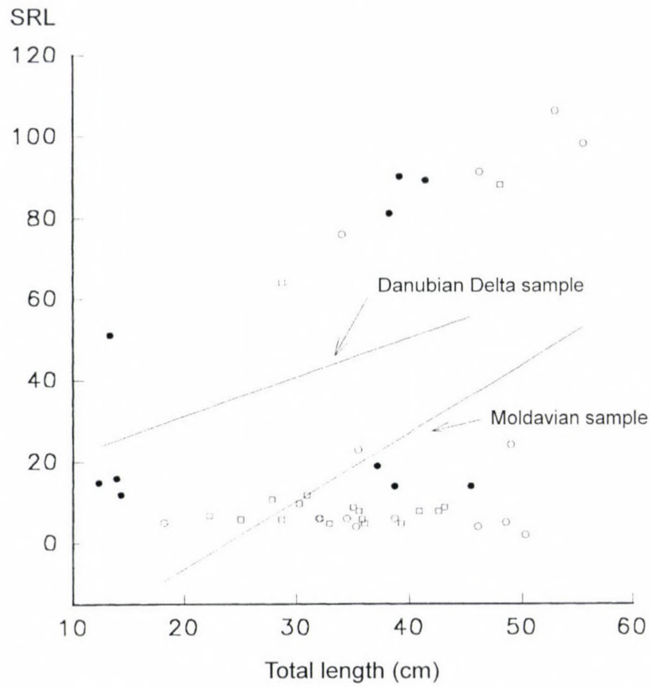


Fig. 7. Dorsal scale row reduction (SRL) from 21 to 19 rows, plotted against corresponding ventral plate number in *moldavica* of different sizes. The two lines indicate the regression through data for the total samples from Danube Delta in Romania and from Romanian Moldavia respectively. Filled circles are specimens from Danube delta, the remaining open symbols are specimens from Romanian Moldavia (Valea lui David = circles; Romanesti = squares)

and 16th ventral). In percentage, the mean reduction is nine in *anatolica*, and between four and eight in the European Mountain populations. The Armenian viper, *eriwanensis*, is most similar to *renardi* in this character while both *tienshanica* and *ebneri* have a somewhat earlier reduction (between ventrals 63 and 96). One specimen of *tienshanica*, from Tacheng Xian, China, has a reduction at level of 65th ventral, and one specimens from Tchinas, Uzbekistan, has a reduction at the level of 63rd ventral. A single specimen of *ebneri* from the Lar valley, Elburs, Iran, has the reduction already at the level of ventral 18. The Caucasian taxon, *lotievi*, is extremely variable, the reduction occurring from level of ventral 17 up to 106, although most specimens are in the upper part of that range. Extreme and comparable with the European Mountain taxa is *parursinii*. It has a mean reduction to 19 scale rows at ventral number 8.81 (ranging between ventrals 5 and 27), and thus with 19 scale rows both at the neck and at midbody. Mean level in percentage of ventral number is 6.5 in this taxon, sexes pooled.

Table 14. Number of dorsal scales one head length anterior to anal in males. Given as mean±S.E., and range, and tested for differences in posterior scale rows with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	17.00±0.00	17	6, 7
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	16.83±0.11	16–17	6, 7
4. *V. u. ursinii* (Italy)	11	16.27±0.30	15–17	7
5. *V. u. moldavica*	20	16.35±0.21	15–17	7
6. *V. u. macrops*	21	15.57±0.20	14–17	1–3, 9–12, 15–17
7. *V. u. graeca*	8	15.00±0.38	13–17	1–5, 9–12, 15–17
8. *V. anatolica*				
9. *V. eriwanensis*	26	17.00±0.06	16–18	6, 7
10. *V. ebneri*	8	17.00±0.00	17	6, 7
11. *V. lotievi*	6	17.00±0.00	17	6, 7
12. *V. renardi*	31	17.00±0.00	17	6, 7
13. *V.* 'west-*renardi*'	18	17.00±0.00	17	
14. *V.* 'east-*renardi*'	13	17.00±0.00	17	
15. *V. renardi* taxon (Altai)	5	17.00±0.00	17	6, 7
16. *V. r. tienshanica*	15	17.06±0.11	16–18	6, 7
17. *V. r. parursinii*	15	17.00±0.00	17	6, 7

The ranges of level of reduction in ventral numbers are for *rakosiensis* 4–100, for *ursinii* 4–14, for *moldavica* 2–106, for *macrops* 2–10, for *graeca* 3–9, for *renardi* 65–127, for 'west-*renardi*' 71–113, for 'east-*renardi*' 65–127, for *eriwanensis* 82–109, for *ebneri* 18–96, for *lotievi* 17–106, for *anatolica* 6–16, for *tienshanica* 63–93, and for *parursinii* 5–27, pooled for both sexes.

The variation within the complex is statistically significant between some taxa (see Tables 16 and 17).

Shape of the rostral (Table 18). There is a certain variation in this characteristic in all taxa, but in four (*eriwanensis*, *lotievi*, *ebneri*, and *anatolica*) the rostral index has a much higher value, i.e. the rostral plate is much higher than broad. Single specimens of 'east-*renardi*' can also show a similar pattern. In the remaining taxa, the rostral plate is about as high as broad.

Number of apicals (Table 19). A single apical plate is the typical state for *ursinii* s. l., and this is the common situation in the taxa and populations discussed here. But, for one taxon, *eriwanensis*, there is a high proportion of specimens that have two apicals, and the mean value is 1.27 for the whole sample, i.e. 27.3% of the

specimens have two apicals. There seems as well to be a certain geographic variation in this character in *eriwanensis*. In the total Turkish sub-sample 36.4% have two apicals, which is also the situation in the single largest Turkish population sample (Asbua, N=17). Corresponding figures for the Armenian sub-sample is 25.0%. The Turkish population at Kagizman has the highest fraction of specimens with two apicals (42.9%), but the sample is rather small (N=7). The variation between *eriwanensis* and some other taxa is statistically significant (see Table 19).

Number of supralabials (Tables 20–21). The number of supralabials spans from 10 (in male *macrops*) to 20 (in *eriwanensis* and male *moldavica*) and 22 (in female *parursinii*) (counted as sum of left and right sides of head) in single specimens. The highest mean value is found in the 'Altai form of *renardi*' (population 15 in Table 21) (X=18.33) and the lowest in *graeca* (X=12.50). In lowland populations, there is a clinal increase from west towards east, with lowest numbers in *rakosiensis*, increasing numbers in *moldavica* and west *renardi*, and with the highest numbers in east *renardi*. To some extent, this parallels the situation in mountain populations (Table 46).

Table 15. Number of dorsal scales one head length anterior to anal in females. Given as mean±S.E., and range, and tested for differences in posterior scale rows with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	16.86±0.08	15–17	7
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	16.95±0.04	16–17	7
4. *V. u. ursinii* (Italy)	18	16.61±0.16	15–17	7
5. *V. u. moldavica*	23	16.78±0.17	15–19	7
6. *V. u. macrops*	20	16.70±0.21	15–19	7
7. *V. u. graeca*	5	15.40±0.24	15–16	1–6, 9–17
8. *V. anatolica*	4	16.75±0.25	16–17	
9. *V. eriwanensis*	21	17.00±0.00	17	7
10. *V. ebneri*	8	17.14±0.13	17–18	7
11. *V. lotievi*	12	17.00±0.00	17	7
12. *V. renardi*	23	17.04±0.04	17–18	7
13. *V.* 'west-*renardi*'	11	17.00±0.00	17	
14. *V.* 'east-*renardi*'	12	17.08±0.08	17–18	
15. *V. renardi* taxon (Altai)	6	17.00±0.00	17	7
16. *V. r. tienshanica*	4	17.00±0.00	17	7 (P=0.058)
17. *V. r. parursinii*	15	16.93±0.07	16–17	7

Table 16. Level of scale row reduction, in males, from 21 to 19 dorsal scale rows. Given as % of all ventrals, and with mean±S.E., and range. Tested for differences in level of reduction in dorsal scale rows with males of other taxa (in % of ventral numbers) (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean level of reduction (in % of ventral number)±S.E.	Range of level of reduction (in % of ventral number)	P≤0.05
1. *V. u. rakosiensis*	23	21.04±4.10	6–66	6, 9–12, 15, 16
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	6.00±0.44	3–8	9–12, 15, 16
4. *V. u. ursinii* (Italy)	11	5.18±0.62	3–8	9–12, 15, 16
5. *V. u. moldavica*	20	12.10±4.19	3–68	9–12, 15, 16
6. *V. u. macrops*	21	4.14±0.28	2–6	1, 9–12, 15, 16
7. *V. u. graeca*	8	4.87±0.58	2–7	9–12, 15, 16
8. *V. anatolica*				
9. *V. eriwanensis*	26	67.84±0.82	58–74	1, 3–7, 17
10. *V. ebneri*	8	62.37±3.00	50–74	1, 3–7, 17
11. *V. lotievi*	6	70.66±1.23	67–76	1, 3–7, 17
12. *V. renardi*	31	64.55±1.20	50–76	1, 3–7, 17
13. *V. r. renardi* (west)				
14. *V. r. renardi* (east)				
15. *V. renardi* taxon (Altai)	5	60.80±0.97	59–64	1, 3–7, 17
16. *V. r. tienshanica*	15	58.61±2.17	46–72	1, 3–7, 17
17. *V. r. parursinii*	15	5.86±0.42	4–10	9–12, 15, 16

Largest variation is found between the different populations of *macrops*, where the number spans over nine supralabials (from 10 to 18). In all other taxa, the variation spans over seven or fewer supralabials. The variation within the complex is statistically significant between some taxa (see Tables 20 and 21). There is no sexual dimorphism expressed in this character.

Number of sublabials (Tables 22–23). The numbers of sublabials span from 14 (in *graeca*) to 25 (in *eriwanensis*) (counted as sum of left and right sides of head). The highest mean value is found in *tienshanica* and *anatolica* (21.00) and the lowest in male *graeca* (15.75). Largest variation is found between the different populations of *eriwanensis*, where the number spans over nine (from 17 to 25). In all other taxa, the variation span is lower. Here the *tienshanica* has the lowest variation with a total span of two and three sublabials respectively. The variation within the complex is statistically significant between some taxa (see Tables 22 and 23). There is no sexual dimorphism expressed in this character.

Number of circumoculars (Tables 24–25). The number of circumoculars spans from 12 (in male *macrops*) to 22 (in *moldavica, eriwanensis*, *lotievi*, east-*renardi* and *tienshanica*) (counted as sum of left and right sides of head). One female of *eriwanensis* has an extraordinary low value of six (three on each side). The highest mean value is found in *parursinii* (X=20.07) and the lowest in *macrops* (X=16.07). Again, the largest variation is found between the different populations of *eriwanensis*, where the number spans over 17 scales (from 6 to 22). However, all specimens of this taxon, except one extreme, have 15 or more circumoculars, equal to a total variation span of eight. In *macrops*, there is also great variation (10). In all other taxa, the variation span is lower. Here female *parursinii* and the 'Altai form of *renardi*' have the lowest variation with a total span of three and two circumoculars, respectively. The variation within the complex is statistically significant between some taxa (see tables 24 and 25).

Number of loreals (Tables 26–27). The number of loreals spans from as few as two (in specimens of *rakosiensis, ursinii, macrops*, and *graeca*) to as many as 18 (in specimens of *eriwanensis*) (counted as sum of left and right sides of head). The highest mean value is found in *parursinii* (10.93), and the lowest in *graeca* (3.9).

Table 18. Rostral index (height/width). Given as mean±S.E. and range

Taxa	N	Mean±S.E.	Range
1. *V. u. rakosiensis*	62	1.01±0.01	0.83–1.15
2. *V. u. ursinii*	65	1.02±0.01	0.83–1.21
3. *V. u. ursinii* (France)			
4. *V. u. ursinii* (Italy)			
5. *V. u. moldavica*	43	1.02±0.01	0.91–1.14
6. *V. u. macrops*	42	1.02±0.01	0.92–1.14
7. *V. u. graeca*	13	0.99±0.01	0.87–1.07
8. *V. anatolica*	3	1.27±0.14	0.87–1.50
9. *V. eriwanensis*	46	1.23±0.02	0.79–1.67
10. *V. ebneri*	16	1.18±0.02	1.05–1.40
11. *V. lotievi*	13	1.11±0.03	0.92–1.27
12. *V. renardi*	59	1.04±0.01	0.91–1.32
13. *V. r. renardi* (west)	26	1.04±0.01	0.95–1.20
14. *V. r. renardi* (east)	30	1.04±0.02	0.91–1.32
15. *V. renardi* taxon (Altai)	6	1.05	0.92–1.33
16. *V. r. tienshanica*	19	1.05±0.02	1.00–1.32
17. *V. r. parursinii*	31	1.03±0.01	1.00–1.16

The largest variation is found between the different populations of *eriwanensis*, where the loreals span over 14 in number (from 5 to 18). In all other taxa, the variation span is lower. Here, the 'Altai form of *renardi*' has the lowest variation with a total span of three loreals.

Further, this is a character that shows strong sexual dimorphism (see Tables). In all taxa females have a higher average than males. This is most pronounced in the 'Altai form of *renardi*', where females have 10.7 loreals in average and males only 5.8. In addition, their ranges do not even overlap.

The variation in this character within the complex is statistically significant between some taxa (see Tables 26 and 27).

Number of second chinshields (Table 28). The number of second chinshields spans from three (in *graeca*) to eight (in *renardi* and *rakosiensis*). The highest mean value is also found in *rakosiensis* (5.52) and the lowest in *parursinii* and the 'Altai form of *renardi*' (4.00), *ebneri* (4.06) and *eriwanensis* (4.11). ANOVA-based pairwise comparison (Scheffe's F test for Post-Hoc comparison) of the involved taxa gave statistically significant differences (P≤0.05) between female *rakosiensis* and females of both French and Italian *ursinii*, as well as among females of *macrops, ebneri, eriwanensis, parursinii*, and the 'Altai form of

Table 18. Rostral index (height/width). Given as mean±S.E. and range

Taxa	N	Mean±S.E.	Range
1. *V. u. rakosiensis*	62	1.01±0.01	0.83–1.15
2. *V. u. ursinii*	65	1.02±0.01	0.83–1.21
3. *V. u. ursinii* (France)			
4. *V. u. ursinii* (Italy)			
5. *V. u. moldavica*	43	1.02±0.01	0.91–1.14
6. *V. u. macrops*	42	1.02±0.01	0.92–1.14
7. *V. u. graeca*	13	0.99±0.01	0.87–1.07
8. *V. anatolica*	3	1.27±0.14	0.87–1.50
9. *V. eriwanensis*	46	1.23±0.02	0.79–1.67
10. *V. ebneri*	16	1.18±0.02	1.05–1.40
11. *V. lotievi*	13	1.11±0.03	0.92–1.27
12. *V. renardi*	59	1.04±0.01	0.91–1.32
13. *V. r. renardi* (west)	26	1.04±0.01	0.95–1.20
14. *V. r. renardi* (east)	30	1.04±0.02	0.91–1.32
15. *V. renardi* taxon (Altai)	6	1.05	0.92–1.33
16. *V. r. tienshanica*	19	1.05±0.02	1.00–1.32
17. *V. r. parursinii*	31	1.03±0.01	1.00–1.16

renardi'. In males, *rakosiensis* differ statistically from Italian *ursinii, macrops, renardi, ebneri, eriwanensis* and *parursinii*.

The largest variation is found between the different lowland populations of *rakosiensis* and *renardi* respectively, where the number spans over five in both taxa (from 4 to 8). In all other taxa, the variation span is lower. Here *anatolica* and *ebneri* have a low variation with a total span of two chinshields, while *parursinii* and the 'Altai form of *renardi*' have no variation at all.

Number of mental scales (Table 29). The number of mental scales spans from two (in *macrops*) to nine (in *ursinii*). The highest mean value is found in *ebneri* (4.87) and the lowest in *graeca* and *macrops* (less than 3.5). The largest variation is found between the different populations of *ursinii*, where the number spans over seven (from 3 to 9). The Alpes Maritimes population of *ursinii* has the highest single mean value in this character (5.83). In all other taxa, the variation span is lower. Here *anatolica* has no variation, but the sample size is very small (n=4). The 'Altai form of *renardi*', and *lotievi* have the second lowest variation with a total span of two gulars.

Table 19. Number of apicals. Given as mean±S.E., and range (in % of specimens with two plates), and tested for differences in apicals between taxa (Fisher's Post Hoc test (PLSD))

Taxa	N	Mean±S.E.	%	P≤0.0008
1. *V. u. rakosiensis*	64	1.09±0.04	9.4	
2. *V. u. ursinii*	65	1.11±0.04	10.8	
3. *V. u. ursinii* (France)	35	1.11±0.06	11.4	
4. *V. u. ursinii*(Italy)	30	1.10±0.07	10.0	
5. *V. u. moldavica*	44	1.02±0.02	2.3	9
6. *V. u. macrops*	44	1.00±0.06	2.3*	9
7. *V. u. graeca*	13	1.08±0.08	7.7	
8. *V. anatolica*	4	1.00±0.00	0	
9. *V. eriwanensis*	47	1.26±0.06	25.5	5, 6, 11–14, 17
10. *V. ebneri*	16	1.00±0.00	0	
11. *V. lotievi*	19	1.00±0.00	0	9
12. *V. renardi*	59	1.04±0.03	4.4	9
13. *V. r. renardi* (west)	29	1.03±0.03		9
14. *V. r. renardi* (east)	27	1.06±0.04		9
15. *V. renardi* taxon (Altai)	10	1.00±0.00	0	
16. *V. r. tienshanica*	19	1.05±0.05	5.3	
17. *V. r. parursinii*	31	1.00±0.00	0	9

* No specimen with two apicals, but one with three. Also two specimens with no apical – thus 6.8% total with more than one, or without apical.

ANOVA-based pairwise comparison (Scheffe's F test for Post-Hoc comparison) of the involved taxa gave statistically significant differences (P≤0.05) between female *rakosiensis* and *macrops*. Male Italian *ursinii* differ statistically from *rakosiensis, moldavica* and *eriwanensis*. Males of *macrops* differ from *moldavica, ebneri* and *eriwanensis*, while males of *graeca* differ from males of *rakosiensis, moldavica, ebneri* and *eriwanensis*.

Notable is that the French and Italian samples of *ursinii* show statistically differences in this character (p=0.0004), when using Fisher's Post Hoc test (PLSD)) (see Taxonomic Account).

Number of crown scales (Tables 30–31, Fig. 8). The number of intercanthal and intersupraocular scales spans from five (in *macrops*) to 22 (in *tienshanica*). The highest mean value is found in female 'Altai form of *renardi*' (14.50). As a rule, the eastern taxa all have a higher fragmentation. The taxon *moldavica* has a mean value of 11.91 (with sexes pooled), but taking the Danube Delta populations alone this sub-sample has the high value of 14.22, with the range going from 11 to

Table 20. Number of supralabials* in males. Given as mean±S.E., and range. Tested for differences in number of supralabial scales with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	15.82±0.19	14–17	5–7, 9–10, 12, 15, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	16.08±0.08	16–17	7, 9, 12
4. *V. u. ursinii* (Italy)	11	15.90±0.16	15–17	7, 9, 12, 15
5. *V. u. moldavica*	20	17.10±0.27	16–20	1, 7
6. *V. u. macrops*	21	15.28±0.35	10–18	1, 7, 9–10, 12, 15–17
7. *V. u. graeca*	8	12.50±0.27	12–14	All
8. *V. anatolica*				
9. *V. eriwanensis*	26	18.00±0.10	17–20	1–4, 6–7
10. *V. ebneri*	8	17.75±0.16	17–18	1, 6–7
11. *V. lotievi*	6	16.83±0.31	16–18	7
12. *V. renardi*	31	17.71±0.14	14–18	1–4, 6–7
13. *V. r. renardi* (west)	18	17.67±0.22	17–18	
14. *V. r. renardi* (east)	13	17.77±0.12	17–18	
15. *V. renardi* taxon (Altai)	5	18.20±0.20	18–19	1, 4, 6–7
16. *V. r. tienshanica*	15	17.46±0.21	16–18	6–7
17. *V. r. parursinii*	15	17.26±0.21	16–18	1, 6–7

* Counted as sum of both sides.

18. The lowest mean value is found in *macrops*. The largest variation is found between the different populations of *tienshanica*, where the number spans over 15 scales (from 8 to 22). The most variable single population in the entire material is the Austrian Grammat/Neusiedle population of *rakosiensis*, which ranges from 7 to 20 crown scales, a span of 14 scales. In all other taxa, the variation span is lower. The lowest span of variation (2) is found in female *graeca* and male *parursinii*.

The total mean for the entire investigated material is around 12, and this could be considered as the normal state. Six taxa, *anatolica*, *eriwanensis*, east-*renardi*, the 'Altai form of *renardi*', *tienshanica* and *parursinii* are situated well above this median, showing a higher degree of fragmentation in this character (as in several other characters). These are both mountain and lowland taxa, as is *macrops*, which shows the lowest degree of fragmentation (as in several other scale characters), well below the normal state in the complex.

Table 21. Number of supralabials* in females. Given as mean±S.E., and range. Tested for differences in number of supralabial scales with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	15.55±0.18	13–18	5, 7, 9–12, 15, 17
2. *V. u. ursinii*				
3. *V. u.ursinii* (France)	23	16.26±0.21	14–18	7, 9–10, 12, 15, 17
4. *V. u.ursinii* (Italy)	18	15.94±0.10	15–17	7, 9–10, 12, 15, 17
5. *V. u. moldavica*	23	16.87±0.22	15–18	1, 6–7
6. *V. u. macrops*	20	15.45±0.27	12–17	5, 7, 9–12, 15, 17
7. *V. u. graeca*	5	12.80±0.49	12–14	All
8. *V. anatolica*	4	16.00±0.82	14–18	7
9. *V. eriwanensis*	21	18.04±0.13	17–20	1–4, 6–7
10. *V. ebneri*	8	18.25±0.16	18–19	1–4, 6–7
11. *V. lotievi*	12	17.50±0.23	16–18	1, 6–7
12. *V. renardi*	24	18.13±0.10	14–19	1–4, 6–7
13. *V. r. renardi* (west)	11	18.00±0.13	17–19	
14. *V. r. renardi* (east)	13	18.23±0.12	18–19	
15. *V. renardi* taxon (Altai)	6	18.33±0.21	18–19	1–5, 7
16. *V. r. tienshanica*	4	17.50±0.50	16–18	7
17. *V. r. parursinii*	15	18.06±0.30	17–22	1–4, 6–7

* Counted as sum of both sides

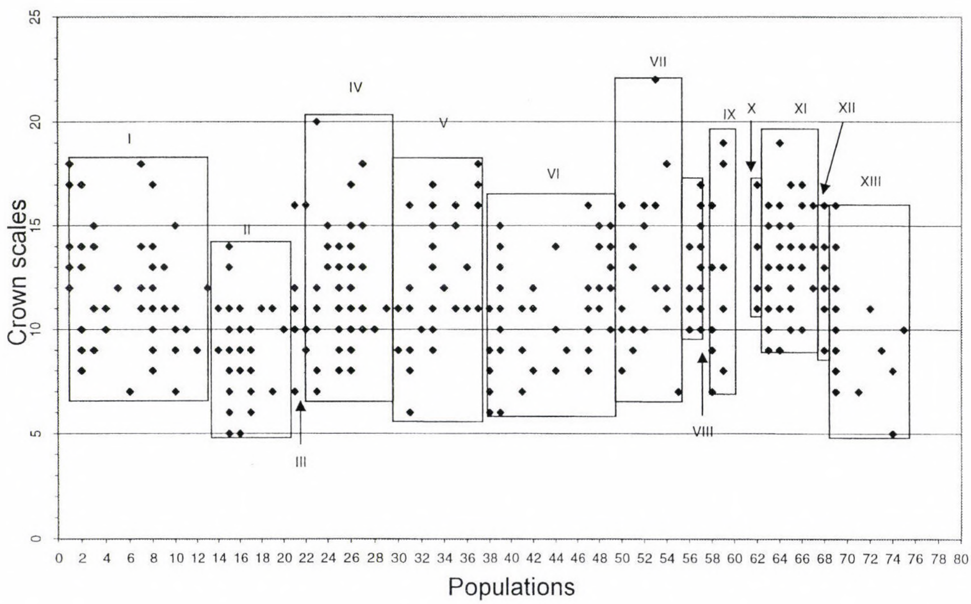


Fig. 8. Distribution of crownscale numbers (intercanthalia + interocularia) in the different investigated populations. Each dot can represent several individuals. Population numbers as in Table 2. Roman numbers indicating taxonomic divisions (I=*ursinii*; II=*macrops*; III=*graeca*; IV=*rakosiensis*; V=*moldavica*; VI=*renardi*; VII=*tienshanica;* VIII=*parursinii*; IX= *renardi* taxon (Altai form); X= *anatolica*; XI= *eriwanensis*; XII= *ebneri;* XIII= *lotievi*)

The variation within the complex is statistically significant between *macrops* and a few taxa (seeTables 30 and 31).

Degree of parietal fragmentation (Table 32). The number of specimens with some to extensive degree of fragmentation of the parietals in the entire complex varies between 14.3% in *lotievi* up to 81.8% in *macrops*, 85.7% in *graeca*, 93.3 in *tienshanica* and 100% in *parursinii*. For the last taxon (*parursinii*) the extremity is reached where all examined specimens (N=31) had (almost totally) fragmented parietals. Most mountain taxa have a high proportion of specimens with divided parietals. Normally more than 68% of the snakes have pronouncedly fragmented parietals. Exceptions are *eriwanensis*, *lotievi*, and *anatolica*. In all the lowland taxa, fragmentation is fixed at a lower level, with *moldavica* having the highest number of specimens with divided parietals (53.3%).

Degree of frontal fragmentation (Table 32). The degree of fragmentation of the frontal is much lower than in the parietals. In the entire complex it varies from zero in *anatolica* and *parursinii*, and up to 40.1% in *macrops*, this is by far the

Table 22. Number of sublabials* in males. Given as mean±S.E., and range. Tested for differences in number of sublabial scales with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	19.39±0.29	16–22	3, 7
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	16.91±0.31	16–19	1, 5, 9–12, 16, 17
4. *V. u. ursinii* (Italy)	11	18.00±0.27	16–20	16
5. *V. u. moldavica*	20	19.15±0.34	16–23	3, 7
6. *V. u. macrops*	21	18.61±0.25	16–22	7
7. *V. u. graeca*	8	15.75±0.59	14–18	1, 5–6, 9–12, 15–17
8. *V. anatolica*				
9. *V. eriwanensis*	26	20.03±0.33	17–25	3, 7
10. *V. ebneri*	8	20.25±0.43	18–22	3, 7
11. *V. lotievi*	6	20.83±0.40	20–22	3, 7
12. *V. renardi*	31	20.27±0.22	18–24	3, 7
13. *V. r. renardi* (west)	18	20.38±0.33	18–24	
14. *V. r. renardi* (east)	12	20.08±0.24	18–21	
15. *V. renardi* taxon (Altai)	7	19.00±0.28	18–20	7
16. *V. r. tienshanica*	14	20.21±0.35	20–22	3–4, 7
17. *V. r. parursinii*	15	19.33±0.23	18 –22	3, 7

* Counted as sum of both sides

taxon with the most fragmented plates in this respect. The taxa *rakosiensis* and *ursinii* are characterised by a low proportion of snakes with a fragmented frontal (1.6% and 4.6% respectively). No pattern concerning fragmentation or phenotypic expression could be detected.

Fragmentation of nasalia (Table 33). The degree of fragmentation of the nasal plate is very variable and can be interpreted in several ways. In *graeca* the entire nasal is often divided into two or more minor plates, or fused with some surrounding plates. In the entire complex, a very special feature occurs to different extents, and that is the occurrence or absence of the upper split of the nasal. This split can occur in all taxa except in *graeca*, where the nasal is divided in other fashions. The presence of this split varies from 94.4% (on one or both sides of head) of the snakes in *ursinii* and down to 10.5% in *tienshanica* and 10% in Iparursinii. The latter two are the least fragmented taxa in this respect. Here a clear pattern can be seen as the European taxa have a rather high degree of fragmentation (75.7% (*molda-*

Table 23. Number of sublabials* in females. Given as mean±S.E., and range. Tested for differences in number of sublabial scales with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	19.23±0.21	16–22	6
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	18.00±0.24	15–20	9, 12
4. *V. u. ursinii* (Italy)	18	17.55±0.23	16–20	5, 8–12, 16
5. *V. u. moldavica*	23	19.60±0.27	18–22	4, 6
6. *V. u. macrops*	20	17.40±0.32	15–20	1, 5, 8–12, 16
7. *V. u. graeca*	13	17.00±0.45	16–18	8, 12, 16–17
8. *V. anatolica*	4	21.00±0.71	20–23	4, 6–7
9. *V. eriwanensis*	21	19.81±0.24	18–21	3, 4, 6
10. *V. ebneri*	8	20.25±0.16	19–22	4, 6
11. *V. lotievi*	12	19.91±0.61	15–24	4, 6
12. *V. renardi*	22	20.32±0.20	19–22	3–4, 6–7
13. *V. r. renardi* (west)	11	20.08±0.23	19–22	
14. *V. r. renardi* (east)	11	20.55±0.30	19–22	
15. *V. renardi* taxon (Altai)	7	19.75±0.37	18–21	
16. *V. r. tienshanica*	4	21.00±0.35	20–22	4, 6–7
17. *V. r. parursinii*	15	19.26±0.33	17–22	7

* Counted as sum of both sides

vica) or more). In *renardi* and all the Asian taxa, a lower degree of fragmentation is expressed.

Size of upper preocular (Table 32). The size of the upper preocular varies in the complex, but normally it is large and in contact with the nasal plate. This character has traditionally been given (together with the single rostral) as the characteristic feature for *Vipera ursinii* s. l. However, the proportion of snakes in the different taxa with the upper preocular in contact with nasal on one or both sides of head, varies from the low value of 22.7% in *eriwanensis* to 100% in *anatolica* (N=4). In the other taxa, the proportion varies between 50.0% (in *moldavica*) and 96.8% (in *parursinii*). Thus, this character holds comparatively well for the entire *ursinii* complex except for *eriwanensis*, where only about one fifth of the snakes expresses this character.

Dorsal pattern (Tables 34–35, Fig. 9). The number of windings, turns, or blotches in the dorsal longitudinal band range from 34 (*anatolica*) to 81 (*lotievi*).

The variation within the complex is statistically significant (df=14, F-value 26.277, P<0.001).

The highest mean values are found in males, with the highest in *lotievi* (70.80), followed by the 'Altai form of *renardi*' (69.00) and *eriwanensis* (65.80). The lowest mean value (38.00) is found in *anatolica*, which also has the lowest degree of variation (9), but then again, this sample is rather small (4). In most cases males have more windings than females, thereby showing some sexual dimorphism. However, in some cases, as in *graeca* and *macrops*, there is no difference.

There is a comparatively large variation within taxa, with a normal variation span of up to about 20 windings. Unique are *anatolica* and *tienshanica*, which through their low number of windings, differ significantly from most other compared taxonomic units. In this character, *anatolica* also differs significantly from the geographically close *graeca* and *macrops*.

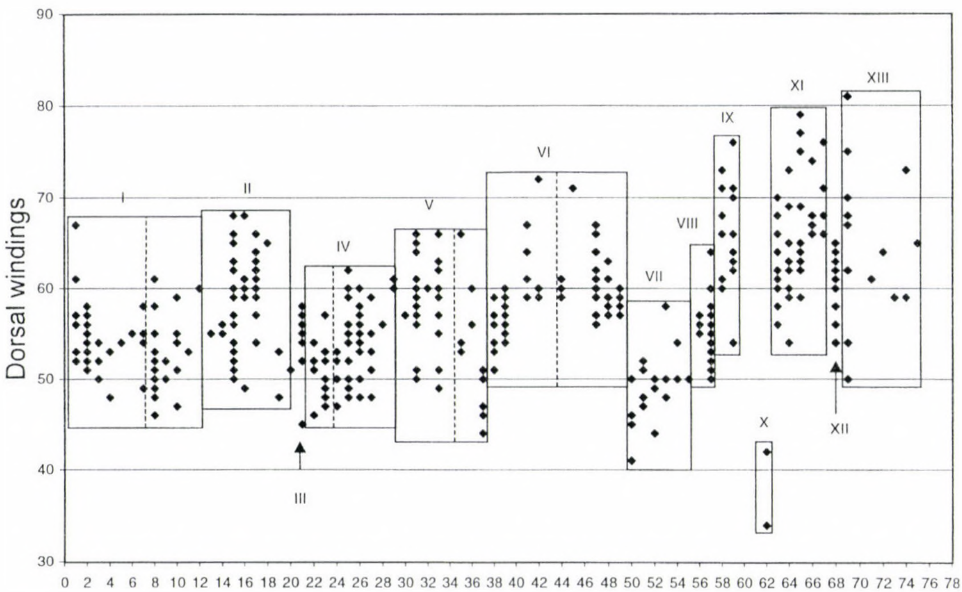


Fig. 9. Number of dorsal windings and markings in the different investigated populations and taxa. Dotted lines separate arbitrary geographical subsamples (in parentheses). Population numbers as in Table 2. (I=*ursinii* (France; Italy); II=*macrops*; III=*graeca*; IV=*rakosiensis* (Austria; Hungary); V=*moldavica* (Bulgaria and Romanian Moldavia; Danube Delta); VI=*renardi* (Ukraine/Russia ="western *renardi*"; Kazakhstan ="eastern *renardi*"); VII=*tienshanica;* VIII=*parursinii*; IX= *renardi* taxon (Altai form); X= *anatolica*; XI= *eriwanensis*; XII= *ebneri;* XIII= *lotievi*)

In *lotievi*, unicoloured, "bronze" specimens also occur. Four out of 16 had this colour pattern. A pronounced bilinear dorsal pattern is also frequent ("*seoanei*-type"), a morph that can also be rarely observed in *eriwanensis*. A longitudinal banded pattern can also be seen in *graeca* (see NILSON & ANDRÉN 1988). A dorsal pattern of isolated blotches, circles, or transverse rectangular bars is frequent in *renardi*.

In spite of reports in the literature of the occurrence of melanistic specimens, no such morphs were recorded. A single specimen of *macrops* had a dorsal, but not lateral black colour. A melanistic specimen of supposed *renardi* from Ukraine turned out to be a *Vipera berus*. Presumed melanistic specimens from Caucasus have always been black specimens of *Vipera dinniki* or *Vipera kaznakovi*. However, a pre-Caucasian population of *renardi* with melanistic specimens is reported from the Krasnodar Region, Southern Russia (OSTROVSKIKH 1997).

There is a significant difference in number of windings between some taxa (see Tables 34 and 35).

Table 24. Number of circumoculars* in males. Given as mean±S.E., and range, and tested for differences in number of circumoculars with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	mean±S.E.	Range	PŁ0.05
1. *V. u. rakosiensis*	23	17.08±0.25	15–20	9, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	17.41±0.23	16–18	17
4. *V. u. ursinii* (Italy)	11	17.63±0.31	16–19	
5. *V. u. moldavica*	20	18.40±0.31	16–22	
6. *V. u. macrops*	21	15.47±0.54	12–21	9, 11, 16–17
7. *V. u. graeca*	8	16.75±0.65	14–20	17
8. *V. anatolica*				
9. *V. eriwanensis*	26	19.34±0.24	17–22	1, 6
10. *V. ebneri*	8	17.62±0.33	16–19	
11. *V. lotievi*	6	19.00±0.82	17–22	6
12. *V. renardi*	31	18.65±0.25	16–21	
13. *V. r. renardi* (west)	18	18.22±0.33	16–21	
14. *V. r. renardi* (east)	13	19.23±0.31	18–21	
15. *V. renardi* taxon (Altai)	5	18.60±0.51	17–20	
16. *V. r. tienshanica*	15	19.20±0.26	16–22	6
17. *V. r. parursinii*	15	20.00±0.20	18–21	1, 3, 6–7

* Counted as sum of both sides

Table 25. Number of circumoculars* in females. Given as mean±S.E., and range, and tested for differences in number of circumoculars with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	17.02±0.25	14–22	17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	17.13±0.19	16–19	17
4. *V. u. ursinii* (Italy)	18	17.27±0.34	14–20	
5. *V. u. moldavica*	23	18.52±0.43	15–22	
6. *V. u. macrops*	20	16.70±0.33	14–20	17
7. *V. u. graeca*	5	16.80±1.02	13–19	
8. *V. anatolica*	4	18.50±0.87	16–20	
9. *V. eriwanensis*	21	17.85±0.64	(6-)16–20	
10. *V. ebneri*	8	17.75±0.31	16–19	
11. *V. lotievi*	12	17.75±0.54	14–21	
12. *V. renardi*	24	19.00±0.36	16–22	
13. *V. r. renardi* (west)	11	17.70±0.41	16–20	
14. *V. r. renardi* (east)	13	20.00±0.41	16–22	
15. *V. renardi* taxon (Altai)	6	19.33±0.21	19–20	
16. *V. r. tienshanica*	4	20.25±0.63	19–22	
17. *V. r. parursinii*	15	20.13±0.17	19–21	1, 3, 6

* Counted as sum of both sides

Ventral colour (Table 36). In general ventral colour follows altitudinal pattern, where lowland populations have dark bellies, while mountain populations have whitish bellies. The figures for specimens with white belly vary between 0% and 13.0% in lowland taxa, like renardi. In mountain taxa, presence of white belly can vary from 71.8% (*eriwanensis*) to 100%. Exceptions are *macrops*, which is intermediate by "only" having 45.2% of the specimens with white belly and the 'Altai form of *renardi*', which, in spite of being a lowland dweller, has white to whitish belly.

Supralabial pattern (Table 33). Normally the snakes in this complex have dark sutures between the supralabials, and especially in *renardi*, this is obvious, as this taxon has very broad dark areas. The proportion of specimens, which lack such a dark suture pattern, vary between none (in several taxa) to all (*graeca, ebneri*). Besides *ebneri*, the other Asian mountain taxa (*lotievi, eriwanensis*, and *anatolica*) also have a low percentage of specimens with dark sutures. The only other exception to this rule is *rakosiensis*, which also has a low frequency of specimens with dark sutures (21.0%).). Thus, it seems not to follow an altitudinal pattern.

Table 26. Number of loreals* in males. Given as mean±S.E., and range, and tested for differences in number of loreals with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	4.91±0.33	2–8	5, 9, 12, 16, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	7.16±0.73	4–11	
4. *V. u. ursinii* (Italy)	11	5.18±0.74	2–10	9, 17
5. *V. u. moldavica*	20	8.20±0.45	4–12	1, 6, 7
6. *V. u. macrops*	21	4.52±0.31	2–7	5, 9, 12, 16, 17
7. *V. u. graeca*	8	3.87±0.58	2–7	5, 9, 12,15, 16,17
8. *V. anatolica*				
9. *V. eriwanensis*	26	9.73±0.56	5–18	1, 4, 6, 7
10. *V. ebneri*	8	7.50±0.46	6–9	
11. *V. lotievi*	6	7.50±0.62	5–9	
12. *V. renardi*	31	8.48±0.32	4–12	1, 6, 7
13. *V. r. renardi* (west)	18	8.44±0.43	6–12	
14. *V. r. renardi* (east)	13	8.54±0.47	4–11	
15. *V. renardi* taxon (Altai)	5	7.00±0.40	6–9	
16. *V. r. tienshanica*	15	8.07±0.64	4–11	1, 6, 7
17. *V. r. parursinii*	15	10.33±0.21	7–12	1, 4, 6, 7

* Counted as sum of both sides

Dorsal head shape (Table 36). The shape of the dorsal side of the head is a very pronounced character that can clearly be seen both in live and in preserved material.

Dorsal side of the snout is often concave resulting in a raised and sharp canthus rostralis. However, there seems to be a geographical connection in the occurrence of this feature. The Asian populations (including *renardi*) have a high percentage of specimens with concave snout, which is not the case for the European taxa. The highest figure is found in 'west-*renardi*' where 88.5% of the examined specimens have concave snout. The lowest figure is found in *ursinii* where only 4.7% of the snakes expressed this feature.

Lateral pattern (Table 33). The normal state of the lateral pattern is distinct lateral spots. In some cases, they can be only weakly expressed. In one case (*graeca*) these lateral blotches are missing or only weakly visible in all snakes examined. In the Asian group of mountain taxa (*eriwanensis, ebneri*, and *lotievi*), this lateral pattern is lacking to a certain degree. In *tienshanica* and *parursinii*, each of the lateral spots consists of a short upper streak only.

Table 27. Number of loreals* in females. Given as mean±S.E., and range, and tested for differences in number of loreals with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	5.52±0.29	2–9	5, 9, 12, 15, 17
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	7.34±0.47	3–12	9, 17
4. *V. u. ursinii* (Italy)	18	7.55±0.54	3–11	
5. *V. u. moldavica*	23	9.13±0.51	6–15	1, 6
6. *V. u. macrops*	20	5.65±0.34	3–9	5, 9, 12, 15, 17
7. *V. u. graeca*	5	4.60±0.68	3–7	9, 15, 17
8. *V. anatolica*	4	9.50±0.26	6–12	
9. *V. eriwanensis*	26	9.73±0.56	5–18	1, 3, 6, 7
10. *V. ebneri*	8	8.37±0.53	7–11	
11. *V. lotievi*	12	8.25±0.66	5–12	
12. *V. renardi*	23	9.45±0.40	6–12	1, 6
13. *V. r. renardi* (west)	10	9.20±0.60	6–12	
14. *V. r. renardi* (east)	13	9.67±0.53	6–12	
15. *V. renardi* taxon (Altai)	6	10.66±0.42	10–12	1, 6, 7
16. *V. r. tienshanica*	4	10.00±0.91	8–12	
17. *V. r. parursinii*	15	10.93±0.18	10–12	1, 3, 6, 7

* Counted as sum of both sides

Analyses of populations

Geographic region analyses

France. A varying number of specimens from seven different French and six Italian populations were examined in this study. In many characters, these different populations are rather similar in external morphology, but a number of differences can be noticed. As is seen from the phylogenetic studies (below) the French populations of *ursinii* seems to have a closer relationship with *rakosiensis* than has Italian *ursinii*. However, in many characteristics, *ursinii* and *rakosiensis* are morphological counterparts, a fact that to a certain extent can be explained by environmental influences on phenotypes, and to an adaptation to different habitats and altitudes.

Despite *rakosiensis* being a sister taxon to *ursinii*, a number of derived character states can be defined in all or most populations of *ursinii*.

Table 28. Number of second chinshields. Given as mean±S.E., and range

Taxa	N	Mean±S.E.	Range
1. *V. u. rakosiensis*	60	5.52±0.13	4–8
2. *V. u. ursinii*	65	4.42±0.09	4–6
3. *V. u. ursinii* (France)	35	4.46±0.14	4–6
4. *V. u. ursinii* (Italy)	30	4.37±0.11	4–6
5. *V. u. moldavica*	43	4.65±0.13	4–6
6. *V. u. macrops*	43	4.23±0.09	4–7
7. *V. u. graeca*	13	4.85±0.30	3–6
8. *V. anatolica*	4	4.25±0.25	4–5
9. *V. eriwanensis*	47	4.11±0.06	4–6
10. *V. ebneri*	16	4.06±0.06	4–5
11. *V. lotievi*	19	4.47±0.19	4–6
12. *V. renardi*	54	4.30±0.10	4–8
13. *V. r. renardi* (west)	29	4.24±0.14	4–8
14. *V. r. renardi* (east)	25	4.37±0.15	4–6
15. *V. renardi* taxon (Altai)	11	4.00±0.00	4
16. *V. r. tienshanica*	19	4.58±0.30	4–7
17. *V. r. parursinii*	31	4.00±0.00	4

* Counted as sum of both sides

The number of ventrals is much lower than in *rakosiensis* (Tables 7–8), and could be considered as an apomorphic state in *ursinii*. However, in the French Alps Maritimes population (Cassoul and adjacent areas)(pop. 7) the number of ventrals is very variable, and specimens with extremely high number (like in *rakosiensis*) are found. On the other hand, the specimen of *ursinii* with lowest ventral number of ventrals (118) originated also from this population. The mean value for this population is 126.0±3.29 S.E. However, the variation within six compared populations in France and Italy was not significant.

In the same way in the Alpes Maritimes population, all examined snakes had 21 dorsal scale rows on the neck. All other populations have 19 or, in two cases, either 19 or 21 (Mt. Ventoux (pop. 1) and Mt. de Lure (pop. 2)). As expected, the level of scale row reduction from 21 to 19 scale rows is more posterior on the neck in this Alpes Maritimes population. These dorsal scalerow characteristics in the Alpes Maritimes population are similar to the situation in *rakosiensis*.

In *rakosiensis* the number of mental scales are comparatively high (X=4.67) while lower in *ursinii* as a whole (X=3.98). Again the French populations of *ursinii* have a higher average value (4.29), and the Alpes Maritimes population has the highest value of all in this characteristic (X=6.40).

Table 29. Number mental scales. Given as mean±S.E., and range

Taxa	N	Mean±S.E.	Range
1. *V. u. rakosiensis*	64	4.67±0.09	4–6
2. *V. u. ursinii*	65	3.98±0.13	3–9
3. *V. u. ursinii* (France)	35	4.29±0.20	3–9
4. *V. u. ursinii* (Italy)	30	3.63±0.12	3–5
5. *V. u. moldavica*	43	4.49±0.14	3–6
6. *V. u. macrops*	42	3.47±0.09	2–5
7. *V. u. graeca*	13	3.46±0.18	3–5
8. *V. anatolica*	4	4.00±0.00	4
9. *V. eriwanensis*	47	4.55±0.10	3–6
10. *V. ebneri*	16	4.94±0.17	4–6
11. *V. lotievi*	19	3.84±0.12	3–4
12. *V. renardi*	54	4.33±0.10	3–6
13. *V. r. renardi* (west)	29	4.31±0.12	3–6
14. *V. r. renardi* (east)	25	4.36±0.16	3–6
15. *V. renardi* taxon (Altai)	11	4.18±0.12	4–5
16. *V. r. tienshanica*	19	3.89±0.16	3–5
17. *V. r. parursinii*	30	4.32±0.10	3–5

* Counted as sum of both sides

In addition, in some colour characteristics the Alpes Maritimes population resembles *rakosiensis*. The belly of several specimens is black, and the supralabials are light, without pronounced dark sutures.

Thus the Alpes Maritimes populations are morphologically heterogenous compared to the Mt. Ventoux and Basse Alp populations. These are to some degree variable in external morphology, but in all main characteristics are typical mountain *ursinii* morphs. As the Alpes Maritimes population shows several similarities with *rakosiensis*, a picture emerges where this population might be more ancestral within the *ursinii* complex. A northwestern branch (the Mt Ventoux and the Basses Alpes populations in France) and a southeastern branch (the Italian populations in the Abruzzo mountain range) may have had their origins from this region.

Italy. No similar degree of variation as in the French populations can be established for the Italian ones, but good series of specimens were only available from two localities (Sibillino Vettore and Gran Sasso (pop. 8 and 10)). The lower limit of the number of loreals is lower (two, counted on both sides) in these two populations compared to the French ones (three). However, the variation between specimens is great and one Italian specimen (from Mt. Velino (pop. 9)) has 11

Table 30. Number of crown scales (intersupraoculars + intercanthals) in males. Given as mean±S.E., and range, and tested for differences in number of crown scales with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	11.30±0.43	7–15	
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	11.66±0.84	8–18	
4. *V. u. ursinii* (Italy)	11	10.54±0.51	9–15	
5. *V. u. moldavica*	20	11.95±0.76	6–18	
6. *V. u. macrops*	21	8.58±0.41	5–14	9, 16
7. *V. u. graeca*	8	10.62±1.03	7–16	
8. *V. anatolica*				
9. *V. eriwanensis*	26	12.73±0.42	9–16	6
10. *V. ebneri*	8	11.87±0.48	9–13	
11. *V. lotievi*	6	9.00±1.07	5–12	
12. *V. renardi*	31	10.48±0.50	7–18	
13. *V. r. renardi* (west)	18	10.11±0.42	7–13	
14. *V. r. renardi* (east)	13	11.00±0.69	8–16	
15. *V. renardi* taxon (Altai)	5	9.60±0.68	8–11	
16. *V. r. tienshanica*	15	12.87±1.00	8–22	6
17. *V. r. parursinii*	15	11.00±0.20	10–12	

loreals. The Italian *ursinii* also has a stronger tendency to have the frontal plate divided.

Bosnia, Croatia, Yugoslavia (Montenegro). A varying number of specimens from eight different populations were examined from this area. Again, there seems to be a great local variation in several morphological characters both within and between populations. However, overall, considering the main morphological character systems, a single taxon (*macrops*) could be defined. The population said to occur on the island of Krk can not be confidently assigned to any particular taxon. Only a single specimen, collected by Bruno, has been available and this specimen shows characters in external morphology that can be found in both *ursinii* and in *macrops*.

This 'upper' Balkan *macrops* is genetically closest to *graeca* in Greece. Of the investigated populations, the one in Cemerno/Bosnia (pop. 16) is in morphology most similar to *graeca*. The Cemerno population has a lower number of supralabials (X=13.14, sum of both sides) compared to the mean value for *macrops* (X=15.26), and this Cemerno value approaches the value of *graeca*

Table 31. Number of crown scales (intersupraoculars + intercanthals) in females. Given as mean±S.E., and range, and tested for differences in number of crown scales with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	12.10±0.46	8–20	
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	11.65±0.62	7–18	
4. *V. u. ursinii* (Italy)	18	10.83±0.44	7–14	
5. *V. u. moldavica*	23	11.87±0.53	8–17	
6. *V. u. macrops*	20	9.30±0.49	5–13	9, 17
7. *V. u. graeca*	5	11.20±0.37	10–12	
8. *V. anatolica*	4	13.50±1.32	11–17	
9. *V. eriwanensis*	21	13.57±0.56	10–19	6
10. *V. ebneri*	8	12.25±0.65	11–16	
11. *V. lotievi*	12	10.75±0.84	7–16	
12. *V. renardi*	24	11.75±0.61	6–16	
13. *V. r. renardi* (west)	11	9.73±0.86	6–15	
14. *V. r. renardi* (east)	13	13.46±0.49	10–16	
15. *V. renardi* taxon (Altai)	6	14.50±1.31	11–19	
16. *V. r. tienshanica*	4	11.75±1.59	9–16	
17. *V. r. parursinii*	15	13.60±0.50	11–17	6

(X=12.62). In addition, the number of ventrals is lower in the Cemerno sample (X=123.6±0.84) than in the rest of *macrops* (X=127.43), and again this is close to the value in *graeca* (X=123.9±0.5). The variation for this character within the complex is statistically significant (df=3, F-value 14,702, P<0.0001). The Greek and Cemerno samples do not differ statistically from each other, but both differ from the other two Bosnian samples (Baba Planina and Korita) (p<0.0001 in all cases). The latter two do not differ statistically from each other. In fact, the Cemerno population could even have been referred to *graeca* on morphological reasons alone. However, there is only 24 km between the type locality for *macrops* (Korita) and Cemerno, but 470 km between *graeca* localities in Greece and Cemerno. In addition, the Cemerno population is situated within the range of *macrops*.

The reduced number of supralabials in these populations is a result of secondary fusion. The specimens with fewer and larger supralabials often retain the dark labial suture pigmentation for a higher number. This phenomenon is especially pronounced in the Cemerno sample.

Table 32. Frequency of certain characteristics in the populations (in %)

Taxa	N	Divided parietals	Divided frontal	Preocular(s) in contact with nasal
V. u. rakosiensis	62	17.7	1.6	69.4
V. u. ursinii	65	78.5	4.6	81.3
V. u. ursinii (France)	34	82.4	2.9	71.4
V. u. ursinii (Italy)	30	76.7	10.0	93.1
V. u. moldavica	46	53.3	17.8	50.0
V. u. macrops	44	81.8	40.1	83.3
V. u. graeca	14	85.7	14.3	84.6
V. anatolica	4	25.0	0.0	100.0
V. eriwanensis	44	20.5	4.5	22.7
V. ebneri	16	68.8	12.5	62.5
V. lotievi	14	14.3	14.3	78.6
V. renardi	57	49.1	14.0	82.4
V. r. renardi (west)	26	42.3	11.5	76.9
V. r. renardi (east)	30	51.7	17.2	82.8
V. renardi taxon (Altai)	14	54.5	54.5	57.1
V. r. tienshanica	15	93.3	33.3	80.7
V. r. parursinii	31	100.0	0.0	96.8

For such reasons, low values in supralabials and in ventrals have been considered as apomorphic states in this study. The results may indicate that the Cemerno population is closer to the ancestor of *graeca* than the other examined 'Yugoslavian' populations. On the other hand, the nearby Korita population of *macrops* (pop. 15) shows morphological trends in the opposite direction. Genetically, *macrops* (together with *graeca*) has a common ancestor with *moldavica* (NILSON *et al.* 1993), and the genetic estimation was based on a Korita specimen. Actually, the Korita population shows several morphological similarities with *moldavica*, such as size. A Korita specimen measured 53 cm in total length, and this is the largest mountain meadow viper found in our entire material. Only the lowland taxa, including *moldavica*, reach a similar size. Furthermore, only in the Korita population were the specimens found with 21 dorsal scale rows on the neck. This is the normal situation in the lowland taxa, including *moldavica*. As a very rare event, a single specimen with 19 dorsal scale rows anterior to the anal was found in the Korita population. The only other taxon in the entire investigated material, where specimens with this high number were found, was *moldavica*. The only *macrops* population with specimens having nine supralabials is the Korita

Table 33. Frequency of certain characteristics in the population (in %)

Taxa	N	Upper nasal split	Supralabial dark sutures	Lateral body blotches missing
V. u. rakosiensis	62	91.8	21.0	0.0
V. u. ursinii	65	94.4	95.4	4.6
V. u. ursinii(France)	35		91.4	9.0
V. u. ursinii(Italy)	30		100.0	0.0
V. u. moldavica	46	75.7	86.7	0.0
V. u. macrops	44	92.0	100.0	0.0
V. u. graeca	14	100.0*	0.0	100.0
V. anatolica	4	66.7	25.0	0.0
V. eriwanensis	44	28.6	53.5	38.6
V. ebneri	16	33.3	0.0	12.5
V. lotievi	14	56.2	28.6	28.6
V. renardi	56	34.3**	100.0	5.5
V. r. renardi (west)	26		100.0	0.0
V. r. renardi (east)	30		100.0	10.7
V. renardi taxon (Altai)	11	25.0	37.5	0.0
V. r. tienshanica	15	10.5	93.3	6.7
V. r. parursinii	31	10.0***	100.0	3.3****

* All investigated specimens have divided nasal plates

** In 12 of 35 specimens examined for this character

*** One out of 31 specimens in this series was malformed in fixation and not included in this character. The three specimens with nasal split all came from the same locality (i.e. three of the four specimens in the Xinyuan Xian sample)

**** In one out of 30 specimens. One specimen was totally black due to formaldehyd fixation and could not be included in this character

population. This is the frequent state in *moldavica*. The individual with highest number of loreals was found in the Korita population (nine, counted as sum of both sides; X=5.02 for *macrops* as a whole; 5.73 for the Korita sample alone). The mean value for *moldavica* is 8.70. In addition, the dorsal head fragmentation is higher in the Korita sample (X= 9.13) than for the taxon as a whole (X=9.05). Corresponding value for *moldavica* is 11.91. Thus, in several characters, of which most have been considered as apomorphic states (see Table 43), the Korita population approaches *moldavica*, and it might be reasonable to consider this population close to the joint ancestral form. Thereby both the events that led to the splitting of the *moldavica* and *macrops–graeca* branch as well as the branching of the *graeca* it-

Table 34. Number of windings or blotches in the dorsal zigzag band in males. Given as mean±S.E., and range, and tested for differences in number of zigzag windings with males of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	23	53.73±1.00	46–62	9, 11–12, 15
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	12	56.83±1.23	50–67	9, 11, 15
4. *V. u. ursinii* (Italy)	11	52.45±1.22	46–60	9, 11, 15
5. *V. u. moldavica*	20	58.25±1.11	47–66	9, 11, 16
6. *V. u. macrops*	21	57.71±1.14	48–68	9, 11, 16
7. *V. u. graeca*	8	52.87±1.85	45–58	9, 11, 15
8. *V. anatolica*				
9. *V. eriwanensis*	26	65.80±0.96	58–77	1–7, 16–17
10. *V. ebneri*	8	60.12±1.62	54–65	11, 16
11. *V. lotievi*	4	70.80±3.58	62–81*	1–7, 10, 12, 16–17
12. *V. renardi*	31	60.06±0.80	53–73	1, 11, 16
13. *V. r. renardi* (west)	18	59.06±1.07	53–72	
14. *V. r. renardi* (east)	13	61.46±1.08	56–71	
15. *V. renardi* taxon (Altai)	5	69.00±2.43	63–76	1–4, 7, 16–17
16. *V. r. tienshanica*	15	48.80±0.63	44–51	5–6, 9–12, 15
17. *V. r. parursinii*	15	56.53±0.72	53–64	9, 11, 15

* Two unicoloured "bronze" specimens excluded

self could have taken place in the same area of Bosnia-Herzegovina. The *macrops* ancestor from the *moldavica* lineage might have entered the Balkan Mountains in this region.

Greece. Only a single Greek population was examined in this study, and in most characters, the span of variation was similar to that observed in other taxa, although in general at a much lower level. For some characters, the variation is greater than normal in this taxonomic complex. The number of circumoculars varies between 13 and 20 (sum of both sides), which is equal to a span of eight. This is more than in most other examined populations where a larger number of specimens have been available for examinations. The mean for 18 such populations is 5.07 and only two populations have a greater span of variation in this character. These are the Caucasian population from Ingushetia (*lotievi*), and the same *macrops* population from Cemerno that was discussed above as being similar to *graeca* in several other aspects!

Table 35. Number of windings or blotches in the dorsal zigzag band in females. Given as mean±S.E., and range, and tested for differences in number of zigzag windings with females of other taxa (ANOVA-based pairwise comparison – Scheffe's F-test for Post-Hoc comparison)

Taxa	N	Mean±S.E.	Range	P≤0.05
1. *V. u. rakosiensis*	38	53.02±0.57	47–60	8-9, 11, 15
2. *V. u. ursinii*				
3. *V. u. ursinii* (France)	23	53.30±0.48	48–57	8–9, 11
4. *V. u. ursinii* (Italy)	18	51.83±0.89	47–61	8–9, 11, 15
5. *V. u. moldavica*	23	56.78±1.29	44–66	8–9
6. *V. u. macrops*	20	58.75±1.13	49–68	8
7. *V. u. graeca*	5	52.80±1.83	46–56	8–9
8. *V. anatolica*	4	38.00±2.31	34–42	1–7, 9–12, 15, 17
9. *V. eriwanensis*	21	64.71±1.36	54–79	1–5, 7–8, 16–17
10. *V. ebneri*	8	60.25±0.86	56–64	8
11. *V. lotievi*	10	62.20±2.12	59–73*	1–4, 8, 16–17
12. *V. renardi*	23	58.00±0.65	51–66	
13. *V. r. renardi* (west)	10	56.45±0.97	51–60	
14. *V. r. renardi* (east)	12	59.42±0.71	57–66	
15. *V. renardi* taxon (Altai)	6	63.16±2.17	54–70	1, 4, 8, 16
16. *V. r. tienshanica*	4	48.75±3.86	41–58	9, 11, 15
17. *V. r. parursinii*	15	53.00±0.62	50–58	8–9, 11

* Three unicoloured "bronze" specimens excluded

The variation between different *graeca* populations could not be investigated.

Austria. A varying number of specimens from two different Austrian populations were examined in this study. Many characters show great variation within populations. In a series of morphological traits there seems to be clinal variation from the west towards the east (when including Hungary, i.e. the whole Carpathian Basin), with the highest values in the east (Figs 10–12). Populations from the westernmost part of this cline (the Austrian populations) have more similarities with the genetically closest relative taxon *ursinii*, than have the eastern part. The Grammat-Neusiedl sample (X=129.6±1.02) differs statistically from three of four compared Hungarian samples (Dabas, Kunpeszér and Pest (X=133.8, 132.1 and 133.7 respectively), as well as from the Sofia sample in Bulgaria (X=135.0±0.00). It does not differ from Ócsa, which has the lowest mean of all Hungarian samples (X=131.3±1.17). As could be expected, it does not differ from the other Austrian sample (Laxenburg: X=132.2±0.86). Morphologically it is most similar with the

Table 36. Frequency of certain characteristics in the populations (in %)

Taxa	N	Snout concave on dorsal side	Belly whitish (not dark)
V. u. rakosiensis	62	14.5	0.0
V. u. ursinii	65	4.7	89.1
V. u. ursinii (France)	35	0.0	82.4
V. u. ursinii (Italy)	30	10.3	96.6
V. u. moldavica	46	36.4	4.8
V. u. macrops	44	7.1	45.2
V. u. graeca	14	23.1	100.0
V. anatolica	4	50.0	100.0
V. eriwanensis	44	51.2	71.8
V. ebneri	16	43.8	87.5
V. lotievi	14	78.6	78.6
V. renardi	57	84.2	20.3
V. r. renardi (west)	26	88.5	7.7
V. r. renardi (east)	30	79.3	37.0
V. renardi taxon (Altai)	15	28.6	86.7
V. r. tienshanica	15	40.0	100.0
V. r. parursinii	31	36.7*	100.0

* Eleven out of 30 in this series; one specimen was malformed during fixation

Alpes Maritimes population of *ursinii* in France. This population and the western *rakosiensis* have the number of mentals, sublabials, dorsal scale rows in the neck region, the level of scale row reduction on body, and the number of ventrals in common.

Hungary. A varying number of specimens from five different Hungarian populations were examined. Again, many characters show little variation between populations although they exhibit great intrapopulational variation. A clinal variation in increasing values in morphology, as stated above, is occurring towards the east (Figs 10–12). The dorsal scale reduction takes place at a more posterior level on the body when going eastwards, and as a consequence the number of dorsal scale rows in the neck region increases in an eastward direction. As stated above, the number of ventrals increases in an eastward direction. The variation in this last character within the Austrian–Hungarian series is statistically significant (df=7, F-value 2,864, P=0.0129).

Romania (Moldavia, Danube Delta region). A varying number of specimens from seven different Romanian populations were examined in this study. To some extent, also the two known Bulgarian populations were included as comparisons. Again a certain intrapopulational variation occurs, but we have not been able to find any large inter-populational variation, in contradiction to what has often been stressed in the literature. Most characters span over the same variation in all populations. However, some clinal patterns can be noticed. The dorsal scale row reduction takes place in a more posterior position on the body in the Danube Delta populations than in the Moldavian ones. The number of sublabials and loreals are slightly higher, and more individuals have a slightly concave head (90% of the Danube Delta specimens, 20% of the Moldavian specimens). There is also a slight increase in the number of ventrals in the Danube Delta populations. The number of dorsal scale rows on the posterior part of the body (X=16.57) is lower in both the Moldavian and the Danube Delta populations, compared to other lowland taxa (X=17.00 in *renardi*, 16.92 in *rakosiensis*). Thereby *moldavica* approaches the ge-

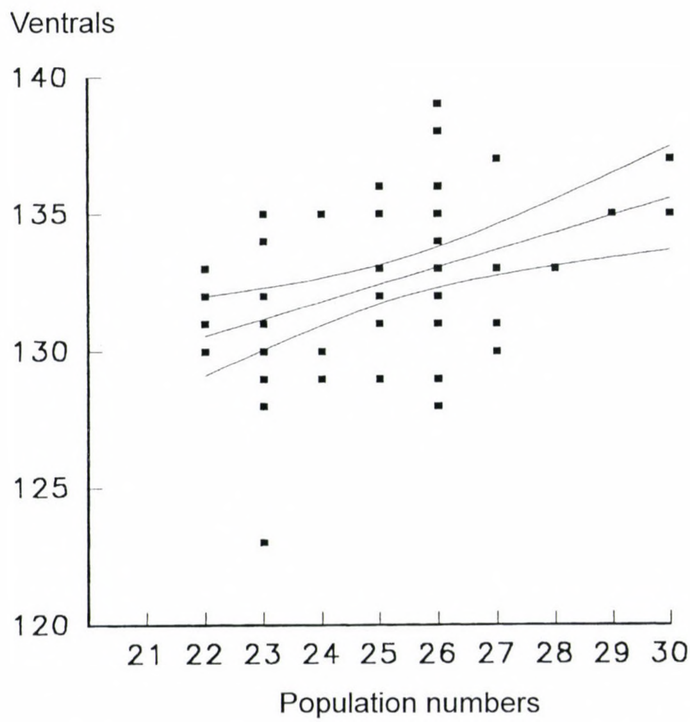


Fig. 10. Changes in number of ventrals in a west – east line through the Austrian and Hungarian populations of *rakosiensis*. The two Bulgarian localities (29 and 30) are included for comparison. Population numbers as in Table 2 and Fig. 1. Regression line through data with 95% confidence intervals indicated.

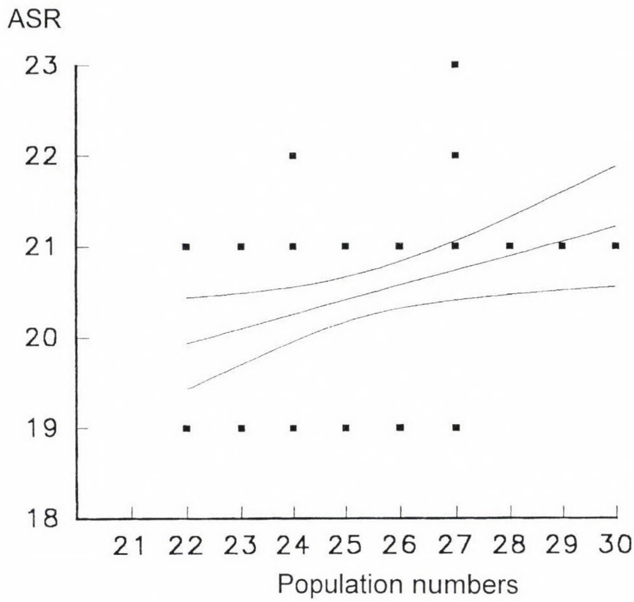


Fig. 11. Number of anterior dorsal scale rows (ASR) counted one head length posterior to head in a west – east line through the Austrian and Hungarian populations of *rakosiensis*. The two Bulgarian localities (29 and 30) are included for comparison. Population numbers as in Table 2. Regression line through data with 95% confidence limits indicated.

netically closest group of taxa (*macrops*, *graeca*) in this character (reduced number of posterior dorsal scale rows is considered as a synapomorphy for these last taxa).

Besides data published by VANCEA *et al.* (1985*a*) and KRECSÁK and ZAMFIRESCU (2001), the single available specimen of the Mt. Rarau population has been examined with the help of a few photos, kindly submitted by Dr. VANCEA. It seems to differ in a similar way as mountain populations do compared to lowland ones. However, the Mt. Rarau habitat (visited in July 1988) only differs from typical Moldavian habitats by its elevation (870 m). In several aspects, the examined individual is similar to *macrops*, e.g. the low ventral count (130) and light belly. In colour pattern, it is rather similar to the specimens (of *moldavica*) from 900 m altitude in the Sofia area, Bulgaria. It seems that these changes in pholidosis in mountain populations represent a phenotypic response to a shift in altitude. This plasticity could be the basis for the evolution of subalpine/alpine populations, where later the alleles became fixed, and submitted to further selection. This might make a better understanding how the taxa *macrops* and *graeca* may have evolved from the

moldavica branch. It might as well constitute the basis for the formation of all mountain taxa from lowland ones.

The two known populations from Bulgaria (possibly extinct nowadays) agree well with the northern lowland populations in pholidosis. We refer them to *moldavica* for various reasons; e.g., the number of zigzag windings is close to that in *moldavica* as is the characteristic broad postocular band.

Russia, Ukraine, North Kazakhstan. A varying number of specimens from 14 different localities were examined from this vast area. The Danube Delta populations in Romania are not included in this sample, as we assign them to the *moldavica* taxon.

The easternmost Kazakh population have highest ventral counts (Dzherzkazgan: X=146.4, Tarbagatai: X=147.5) compared to the rest of the examined *renardi* populations (X=142.93 for all populations together). If we compare the European ones with the Asian ones, the former has a mean value of 141.52 ven-

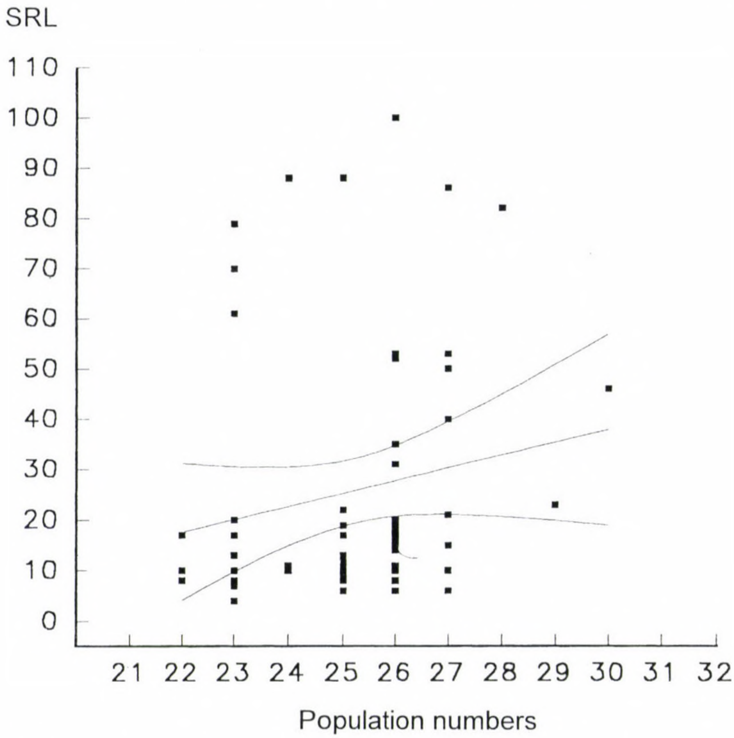


Fig. 12. Level of reduction (SRL) from 21 to 19 dorsal scale rows in a west – east line through the Austrian and Hungarian populations of *rakosiensis*. The two Bulgarian localities (29 and 30) are included for comparison. Population numbers as in Table 2. Regression line through data with 95% confidence limits indicated

trals, while the latter has a mean value of 144.20 ventral scales. It is not possible to see if there is a clinal variation in this character or a real gap. However, the remaining examined specimens from the Kazakh Steppe region and adjacent areas in Asia ("Kazakhstan", Omsk, and Tomsk, Sasykkol) also have high ventral counts, indicating an actual low western and high eastern distribution in ventral numbers. The variation within the *renardi* sample is statistically significant (df=4, F-value 4,309, P=0.0057). Both the West Russian and Ukrainian samples (Dnjepr (pop. 39) and Orlov island (pop. 38)) differ statistically from each of the two compared Kazakh ones (Dzherzkazgan (pop. 47) and Tarbagatai (pop. 49)). As could be expected they do not differ from each other in this character. Neither do the two Kazakh populations differ from each other.

The Kazakh population also shows a greater variation in number of supralabials than compared populations, ranging from 17 to 19. Normally *renardi* has rather constantly 18 supralabials (nine per side of head). However, in the Kislowodsk sample (pop. 42) one specimen had only 14 supralabials (seven on each side).

In the Western Ukrainian populations (Orlov Island, Dnepr), several specimens have an increased dorsal scale count on neck (22 to 23) while 21 is normal for *renardi* as a whole.

Armenian highlands, East Anatolia. A varying number of specimens of *eriwanensis* from seven different localities, arranged in five populations, were examined from this area. In general, most characters vary between certain limits, and there is no pronouncedly divergent population in our examined material. The external morphology in *eriwanensis* is rather constant and symmetrical, indicating a high level of heterozygosity because of high population density. A certain variation between populations can be seen in the shape of the rostral plate, which, however, in general is narrower and higher in this and presumed related taxa (*ebneri, anatolica*) (Table 18).

The number of circumoculars is very variable, normally ranging between 15 and 22 (counted on both sides), but a single specimen from the Asbua sample (pop. 65) has only five circumoculars altogether! The number of loreals is perhaps the most variable character. In the Ara-Iler population (pop. 63), it spans from 5 to 18 in total number, and the other populations have large variation as well. The mean number is 10.13. The fragmentation of the head scales (intercanthals and intersupraoculars) is high in this taxon compared to all others (Tables 30 and 31), with a mean value of 13.37 crown scales in females. This is in agreement with published data (BASOGLU 1949, EISELT 1976). The Asbua sample contained a specimen with secondarily united sub- and supralabials, as was also seen in *macrops*.

Snakes from the vicinity of the northern part of Lake Sevan differ somewhat in body shape and morphology. These snakes have not been included in all analyses because only single specimens were originally available. The three specimens examined differ from other *eriwanensis* samples in having a lower number of ventrals (130–134). Mean value for remaining *eriwanensis* populations is 137.66 (range 133–143). The number of zigzag windings is also lower in the Sevan sample (X=59.0, range 55 to 63) compared with the remaining available *eriwanensis* populations (X=65.32, range 54 to 79).

Iran. Specimens from two north Iranian populations of *ebneri* were examined in this study and, in most characters, the range of variation was similar to that observed in other taxa, and often rather similar to the different populations of *eriwanensis*. The average number of zigzag windings is lower, and the reduction of dorsal scale rows from 21 to 19 is more anterior, with a lower mean number of midbody scale rows. The number of ventrals (X=129.88) is much lower than in *eriwanensis* (X=137.34), and the supralabials are without dark sutures or finely dotted. One specimen has a dark upper suture on an otherwise undivided nasal. The undivided stage could be a plesiomorphy (although environmental influences, such as changing developmental temperatures during embryogenesis, can cause such effects (FOX *et al.* 1961).

Azerbaijan. In Azerbaijan, the situation is rather complex. Members of the *ursinii* complex are occurring in three different regions of the country. There is an eastern/north-eastern group of populations, a southeastern group and a western series (e.g. ALEKPEROV 1978, 1982), and these three separated ranges represent three different taxa, namely *renardi, ebneri* and *eriwanensis*, respectively. The western populations border towards the Armenian series of *eriwanensis*, and the taxon is abundant along the border between these two countries (own obs.) as well as in the Karabakh plateau (2000–3000 m altitude) (ALEKPEROV 1982). These habitats are high mountain steppe habitats. The northern series consists of lowland steppe inhabitants, coming from north along the Caspian Sea lowland areas to the east of the Caucasus. As discussed later, we have had access to a live specimen of *renardi* from the vicinity of the town Shemakha (Shemacha), Azerbaijan, found in a steppe habitat. The southeastern series occurs in the Talysh Mountains, which is south of the Aras River and on the border towards Iran. It is connected with the Iranian range for the taxon *ebneri*.

Caucasus (Russia, Georgia). Specimens are examined from various parts of the Caucasus, and one sample from Ingushetia yielded a larger series of specimens. The Caucasian populations have been described as *Vipera lotievi* (NILSON *et al.* 1994, 1995), and a more comprehensive study is presented in these publications. The expressed intra-populational variation shows that in this investigated popula-

tion the range of variation of the different characters is of the same magnitude as for other taxa. A rather big upper preocular can be seen in several cases. This population also contains unicoloured "bronze" specimens (See Plate 1d, in NILSON *et al.* 1995).

SW Anatolia. A single Taurus Mountain population (the only known) is studied, and only four specimens have been available. This small sample does not allow us to say anything about inter- and intra-populational variation for this taxon (*anatolica*), but see the tables and the figures for numerical values. The morphological differences and similarities compared to other taxa are discussed elsewhere.

Kirgizia, Uzbekistan, South Kazakhstan, West Tien-Shan range in Xinjiang, NW China. A varying number of specimens from eight different localities (samples), arranged in two different taxa, were examined. There is considerable variation between populations, as can be seen when comparing the different populations in this geographical region. The mountain populations are united in the taxon *tienshanica*. The easternmost one, Kuldja (Yining) (pop. 53) is situated in Tien-Shan, Xinjiang, NW China, while the northernmost ones are at Qoqek (pop. 55) and Yumin (pop. 54) SW of the Chinese section of the Tarbagatai Mountains, near the Kazakhstan border. The westernmost population is from Chinas, Uzbekistan (pop. 50). To the north of this range, *renardi* is found. We have examined two populations of typical *renardi* in close connection with the *tienshanica* taxon.

One population comes from Akterek, Alma-Atinsk, Dzambulski, Kazakhstan (pop. 48), and it resembles typical *renardi* in several ways. The number of circumoculars in this Akterek, Dzambulski sample is lower (X=18.4) than for the region as a whole (X=19.21) (19.53 for the other populations alone (=*tienshanica*)) and approaches the value for *renardi* (X=18.77). The same is true for the supralabials (X=18.2), which differ from the value of the region as a whole (X=17.53)(17.33 for the other populations alone (=*tienshanica*)).

Further, the difference is pronounced in the number of zigzag windings in the dorsal band (Fig. 9). Mean for this character is 59.6 (range 57–63) in the Akterek, Dzambulski population, compared to 48.2 (range 41–58) for the rest of the region (=*tienshanica*) (50.68, if the Akterek, Dzambulski sample is included in the region as a whole). In *renardi*, mean value for this character is 59.41, very close to the Akterek, Dzambulski value.

The difference is also pronounced in the number of ventrals (see Fig. 3). In the Akterek, Dzambulski population the mean value is 144.4 compared to 135.00 (range 129–138) for the rest of the region (=*tienshanica*). In *renardi*, mean value for this character is 142.93, again very close to the Akterek, Dzambulski value.

All these eastern mountain populations probably have the eastern lowland *renardi* ("east-*renardi*") as their closest relative. This is similar to all the rest of the

mountain populations in Europe and Asia, which have their closest relatives in the different northern lowland populations. These populations have not been subjected to biochemical investigations, but there are no indications that these eastern mountain populations should diverge from the pattern seen elsewhere. Thus, the Tarbagatai, and the Akterek, Dzambulski populations can either be remnant populations still close to the ancestral *renardi* predecessor that gave rise to the mountain form in this region. It can also belong to this Tien Shan Mountain taxon, but then has secondarily switched back to more typical "*renardi*" morphology (convergent autapomorphy instead of a plesiomorphic stage) for some reason (e.g. altitude change). We believe in the former hypothesis where the Tarbagatai and Akterek, Dzambulski populations have retained the ancestral patterns (plesiomorphy) from the original *renardi* founder populations, and are southeastern distributions of a wide-ranging east-*renardi*.

It seems to be a continuous distribution of *renardi* along the northern foothills of Kazakh-Kirgizian section of Tien Shan. Lowland populations occur in the regions between the mountain range Dzhungarski Alatau and Lake Balkhash at the northeast, and in the Shaldara steppe along Syrdarya River in the southwest. Here the species is a lowland steppe inhabitant according to BANNIKOV *et al.* (1977).

The Akterek, Dzambulski population sample seems to originate near the Frunze sample of *tienshanica*. The latter locality is in the central part of the range of *tienshanica*, and consequently here there is a region of parapatry of *renardi* and *tienshanica*. However, it is also possible that this Akterek, Dzambulski locality is south of the Trans-Ili Alatau, south-east of Almaty. There are several Dzambuls and Aktereks in Kazakhstan, but one of these two localities are believed to be the correct locality for this sample (TATJANA DUJSEBAYEVA, pers. com. and NIKOLAI ORLOV, pers. com.). In any case it is (at least) parapatric with *tienshanica*, which occurs to the west (Almaty) and east (Yining) of this locality.

In the Tarbagatai Mountains further north, the situation is similar, with typical *renardi* in the Western, Kazakh section of the range, and with *tienshanica* in the Chinese eastern part (Yumin and Qoqek). Here *tienshanica* is coming up from the south (Yining) inside China, and again forming a parapatric pattern of distribution. Thus, a pattern emerges with two parallel southwest-northeast distributions in this region. A mountain series (*tienshanica*) is distributed in the Chinese, Kirgizian, Kazakh and Uzbekh sections of Tien Shan, and a lowland steppe series (*renardi*) along the northern foothill steppes of the same mountains. The latter series of true *renardi* is distributed in Kazakhstan only. This parapatry might even be a sympatric, mosaic distribution of the two taxa in this region. The Akterek, Dzambulski material and the West Tarbagatai material are included in the east-*renardi* sample in the following analyses.

East Tien-Shan mountain range (Xinjiang), China. Thirty-one specimens from the two localities Nilka Zian (pop. 57) and Xinyuan Xian (pop. 56) were examined. Specimens from these two sites are very different from the more northern populations in China (*Vipera renardi* s. l., as already demonstrated by ZAO and JIANG (1979). By having 19 dorsal scale rows on neck and at midbody they differ from all other Asian populations of *ursinii* s.lat. They are most similar to the European Alpine populations in this character. They also differ in labial colour pattern, lateral body pattern, pronounced dorsolateral longitudinal lines on distal edges of ventrals, and number of ventrals from traditional *renardi*, as well as from the geographically closest relative: *tienshanica*. The reduced number of scale rows may be a result of an adaptation towards alpine niche choice. This characteristic is comparable with the reduced number of scale rows in the European mountain populations, and which also can be interpreted to some extent in Asian alpine populations, i.e. a case of convergence.

Altai Mountains, east Kazakhstan and nearby China. A number of populations are distributed in the foothills of the Altai Mountains, and these populations differ in a number of morphological characteristics, as well as in habitat preference. These are small snakes, inhabiting lowland rocky slopes and edges, but expressing typical size and colour pattern of mountain '*ursinii*' taxa. These populations seem to be isolated from the parapatric, and likewise lowland inhabiting typical *renardi*. Towards the south of its range is the Zaysan depression, with the Tarbagatai Mountains. Here *renardi* occurs. Further, east of the Zaysan depression the Black Irtish desert and river systems, can have some effect on the dispersal. However, this desert is bordered by the Saur Mountains on its southern side, and we found the 'Altai form of *renardi*' also in these hills. Towards north the high Altai, and towards the west the Irtish river and Kaznakowka sand dune fields prevent dispersal of meadow vipers. Further, the same taxon is also occurring on the Chinese side of the Chinese-Kazakhstan border, at Hababe Xian (Kaba). In China, the Irtish River depression forms a southern limit in the distribution. Thus, on the south side of the Zaysan depression, the Tarbagatai Mountains is inhabited by east *renardi*, and the 'Altai form of *renardi*' inhabits the Saur Mountains. From the south *tienshanica* comes up in the eastern Chinese section of Tarbagatai (at Tacheng and Yumin). Thus, the taxonomic situation is rather complicated in these mountains, where three taxa meet, and shows a parapatric distribution pattern. Towards the east lies the Junggar Pendi desert, towards north the Irtish depression, and towards south the Djungar Gate steppe and desert lowlands. No vipers are recorded from the Djungar Alatau Mountains south of the depression, except a little further south, at Yining (Kulja), Xinjiang, China, where *tienshanica* is found. Thus, these isolated mountain systems, separated by desert lowland plains, are in-

habited by three different taxa: the 'Altai form of *renardi*', east *renardi* and *tien-shanica*. Further into Xinjiang, *parusinii* is found.

Although occurring nearby and almost parapatric they differ in morphology and ecology. *Renardi* is a big taxon, with black belly and blackish supralabials. The other three are small, white-bellied taxa, where *parursinii* has 19 mid-dorsal scale rows, while the other all have 21. *Tienshanica* has few ventrals (129–138), while the 'Altai form of *renardi*' has many (142–150). In addition, the 'Altai form of *renardi*' is a lowland dweller inhabiting rocky slopes, near to water, while all the others (except *renardi*) are mountain inhabitants.

Multivariate Analyses

Principal Components Analysis (PCA), and Canonical Variate Analysis (CVA), on taxon level

The PCA resulted in three, more or less, distinct clusters of individuals with some overlap. The situation was similar but not identical for males and females (Tables 37 and 38, Figs 3–8). Amongst the males, Italian *ursinii*, *macrops*, *graeca*

Table 37. Factor loadings on the first four principal components extracted from a correlation matrix of 15 meristic characters for individual males of all 13 OTUs of the *Vipera ursinii* complex

Characters	PC1	PC2	PC3	PC4
Preventrals	0.272	–0.042	0.672	0.251
Ventrals	0.770	–0.200	–0.134	–0.032
Subcaudals	0.618	–0.006	–0.082	–0.210
SQ-neck	0.772	–0.038	–0.191	0.385
SQ-midbody	0.823	–0.257	0.009	0.276
SQ-posterior	0.650	0.170	0.040	0.116
Level scale row reduction (%)	0.820	–0.291	–0.046	0.309
Supralabials	0.810	0.065	0.042	–0.156
Infralabials	0.643	0.017	0.215	0.097
Circumoculars	0.585	0.298	0.051	–0.332
Loreals	0.603	0.360	0.301	–0.329
2nd chinshields	–0.207	0.464	–0.261	0.602
Mental row	0.345	0.365	–0.618	–0.071
Crown scales	0.286	0.765	0.114	0.004
Zigzag turns	0.459	–0.359	–0.293	–0.355
Eigenvalues	5.647	1.508	1.208	1.187
% Variance explained	37.64	10.05	8.05	7.91

Table 38. Factor loadings on the first four principal components extracted from a correlation matrix of 15 meristic characters for individual females of all 14 OTUs of the *Vipera ursinii* complex

Characters	PC1	PC2	PC3	PC4
Preventrals	0.261	0.112	0.299	0.781
Ventrals	0.795	0.115	0.010	0.117
Subcaudals	0.464	0.282	0.020	0.175
SQ-neck	0.735	0.145	–0.439	0.105
SQ-midbody	0.841	0.216	–0.028	–0.126
SQ-posterior	0.421	0.051	0.011	0.049
Level scale row reduction (%)	0.872	0.227	–0.151	–0.069
Supralabials	0.769	–0.147	0.296	–0.069
Infralabials	0.628	–0.230	–0.184	0.162
Circumoculars	0.432	–0.567	0.313	0.047
Loreals	0.594	–0.410	0.347	–0.177
2nd chinshields	–0.173	–0.233	–0.637	0.474
Mental row	0.311	–0.290	–0.665	–0.309
Crown scales	0.311	–0.663	–0.020	0.018
Zigzag turns	0.470	0.516	0.059	–0.214
Eigenvalues	5.071	1.634	1.499	1.119
% Variance explained	33.80	10.89	9.99	7.46

is here referred to as group X, French *ursinii*,*rakosiensis, moldavica* and *parursinii* as group Y, and *renardi, lotievi, ebneri, eriwanensise, tienshanica* and the 'Altai form of *renardi*' as group Z. Amongst the females French *ursinii*, Italian *ursinii*, *macrops* and *graeca* formed the first cluster (=X), and *rakosiensis, moldavica* and *parursinii* formed the second (=Y), while *renardi, lotievi, ebneri, eriwanensis, tienshanica* and the 'Altai form of *renardi*' formed the third cluster (=Z). These clusters were then entered into the canonical variate analysis (CVA) as *a priori* groups (see below). *V. u. anatolica*, which consists of only 4 female specimens (three of which were separately clustered in the components space), was excluded before putting the data into the CVA.

In order to evaluate the actual degree of discrimination among the three distinct groups (X, Y, Z) resulted from the PCA (see above), these groups were used as *a priori* groups in order to run a CVA. As it is evident the two obtained canonical variates (CV1 and CV2) explain total variation in the data (Tables 39 and 40). In order to display the variation among the *a priori* groups graphically, the individual specimen scores were plotted for the two resultant canonical variates (CV1 and

Table 39. Standardized canonical coefficients for male specimens of 13 OTUs of the *Vipera ursinii* complex belonging to three a priori groups

Characters	CV1	CV2
Preventrals	0.090	0.270
Ventrals	0.202	–0.377
Subcaudals	–0.037	–0.165
SQ-neck	0.039	–0.606
SQ-midbody	–0.373	0.119
SQ-posterior	0.535	–0.420
Level scale row reduction (%)	0.711	0.407
Supralabials	0.257	0.085
Infralabials	–0.217	0.648
Circumoculars	0.190	0.383
Loreals	0.525	–0.006
2nd chinshields	0.102	–0.212
Mental row	0.303	0.128
Crown scales	–0.144	0.122
Zigzag turns	0.010	0.182
Eigenvalues	8.86	2.89
% Variance explained	75.40	24.60

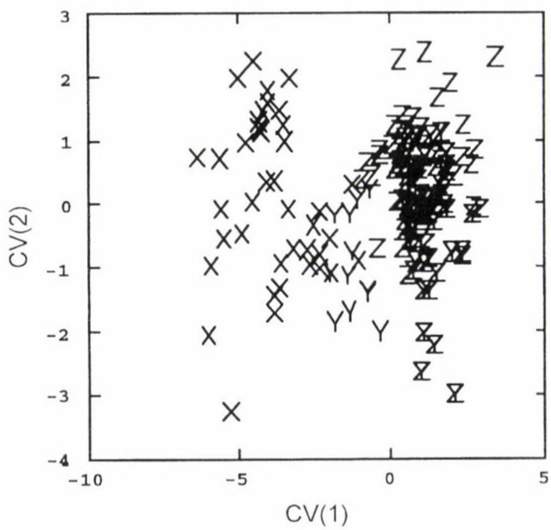


Fig. 13. Plot of individual males of 13 OTUs of the *Vipera ursinii* complex belonging to three *a priori* groups on the first two canonical variates

Table 40. Standardized canonical coefficients for female specimens of 13 OTUs of the *Vipera ursinii* complex belonging to three a priori groups

Characters	CV1	CV2
Preventrals	0.131	0.022
Ventrals	0.536	0.587
Subcaudals	0.027	0.149
SQ-neck	–0.043	0.257
SQ-midbody	0.371	–0.378
SQ-posterior	–0.086	0.110
Level scale row reduction (%)	0.146	–0.218
Supralabials	0.287	–0.310
Infralabials	0.251	0.298
Circumoculars	–0.073	–0.126
Loreals	0.105	–0.257
2nd chinshields	–0.100	0.513
Mental row	0.169	0.169
Crown scales	0.093	0.139
Zigzag turns	–0.048	–0.150
Eigenvalues	8.77	7.15
% Variance explained	55.09	44.91

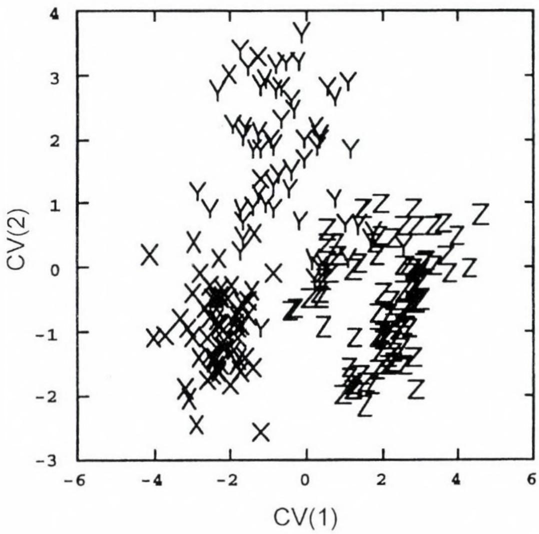


Fig. 14. Plot of individual females of 13 OTUs of the *Vipera ursinii* complex belonging to three *a priori* groups on the first two canonical variates

Table 41. The predicted group membership of individual male specimens belonging to one of the three a priori groups of the *Vipera ursinii* complex by the first two canonical variates using the jack-knifed procedure and Mahalanobis distances

		Predicted group membership			
A priori groups	*n*	X	Y	Z	% Correct
X	40	38	2	0	95
Y	55	3	29	23	52.72
Z	111	0	32	79	71.17
Total	206	41	63	102	% correct overall = 72.96

CV2) for both males and females. As it is shown, in both sexes, especially in females, the three *a priori* groups are rather well separated in the canonical space (Figs 13–14).

In addition, the jack-knifed classification procedure based on a matrix of Mahalanobis distances was used to evaluate the group membership of all the specimens to the group with which they shared the greatest morphological similarity. In both males and females, the Group X showed the greatest morphological distinctiveness. In the overall distinctiveness, females revealed a higher percentage (88.45) than males (72.96) (Tables 41 and 42)

The groupings express morphological similarity, which in turn might reflect a phylogenetic pattern. All eastern taxa, except *parursinii*, are included in the *renardi* lineage (group Z). The other two groups (X and Y) gather the European mountain taxa and the European lowland taxa, respectively. Surprising is the fact that the Chinese male and female *parursinii*, together with French male *ursinii* are in group Y. French female *ursinii* cluster together with the other European mountain taxa in group X.

However, the morphological similarity might also reflect morphological convergence in similar ecological niches, and this in turn may affect the outcome

Table 42. The predicted group membership of individual female specimens belonging to one of the three *a priori* groups of the *Vipera ursinii* complex by the first two canonical variates using the jack-knifed procedure and Mahalanobis distances

		Predicted group membership			
A priori groups	*n*	X	Y	Z	% Correct
X	66	62	4	0	93.93
Y	61	5	47	9	77.04
Z	89	2	3	84	94.38
Total	216	69	54	93	% correct overall = 88.45

of the phenetic analyses. The situation in group Y above, with the European lowland "puszta" and steppe inhabitants' cluster together with the Chinese mountain *parursinii* is clearly such a case. In addition, the sample of French male *ursinii* found its way to this group, which cannot easily be explained with adaptations to similar habitats. On the contrary, this may be a sign of phylogenetic relationship.

In group X above, the European Mountain taxa (except French male *ursinii*) were together. They all occur in the same kind of alpine/subalpine meadow habitats, and their clustering together could well be explained by morphological convergence. In group Z all *renardi* populations, as well as other Central Asian taxa (except *parursinii*) were clustered together. In this case, adaptations to similar habitats can not be the explanation as the group contains taxa adapted to very diverse altitudes and habitats. Rather phylogenetic constrains can be suspected to have given this result. However, these are hypotheses. We cannot demonstrate with these methods what has happened in history. What can be suspected, however, is that both relationships and convergence are involved in the results obtained.

From multivariate studies on local populations, and based on sexes and geography (in preparation) a similar pattern is received. Most of the populations within taxa fall out together indicating morphological similarity. In all taxonomic units, however, one or a few populations differ morphologically. In some cases considerably. In addition, the differences can be more pronounced between populations of the same taxon than between geographically distant ones.

The "strange similarity" between many geographically and supposed genetically distant populations can be explained by convergence in adaptations to a similar environment. Again, there is a tendency for lowland populations to cluster together, and for mountain populations and taxa to cluster together. Occasionally mountain and lowland populations cluster together, but normally when genetically close, or suspected to be so.

There seems to be two different forces acting. Populations or taxa from a similar habitat and/or altitude may have developed a similar pholidosis and cluster together or genetically related populations or taxa cluster together.

Consequently, if we only have morphology at hand it is necessary to act with carefulness when drawing conclusions about the systematics, especially if we are interested in a taxonomy that reflects the evolutionary history. In addition, the phylogenetic information content of the different characters is most variable. In a cladistic analysis, a high rate of homoplasy can be expected, with difficulties in the reconstruction of phylogenies. When defining a certain group of populations into a Linnean taxon the actual morphology expressed here in tables and phenograms is of course valuable and correct to use. This is regardless of whether its expression is derived from the phylogenetic history or phenotypic adaptations. The evolutionary

species in this sense must be defined by its morphology in a traditional way, even if its phylogeny can not be inferred from these criteria.

Consequently, the *ursinii* complex is a systematic entity with strong tendencies towards morphological similarity due to adaptations to similar habitats, and due to phylogenetic constrains. Thus, a number of siblings and cryptic taxa must be expected, and the conclusion has to be drawn that it is difficult to reconstruct the phylogeny on phenetic parameters alone.

PHYLOGENETICS

The cladistic analysis is based on information from the external morphology (Table 3). Altogether 15 characters may contain phylogenetic information (Table 43). The *Vipera ursinii* s. l. taxa have been divided into 15 groups as *ursinii* here is split into French and Italian subsamples, and *renardi* into west and east *renardi* samples (Tables 43 and 45). Further, the Altai population of *renardi* is treated here as a separate taxonomic entity ('Altai form of *renardi*'). Some types of characters, or character states, have been excluded from the phylogenetic analyses. Autapomorphies, discussed elsewhere, and characters that are invariant within the group, are not used. *Vipera berus* is used as outgroup.

As discussed in the Method section certain morphological characters can be modified due to external impact (e.g. temperature during embryogenesis, short season etc.). Consequently, it is possible that some morphological characteristics are adaptations or modifications to similar environments, and thereby do not carry phylogenetic information, i.e. these are convergences.

The same would prevail concerning the various mountain populations. Certain phenetic traits clearly support this hypothesis, e.g. the 19 neck and midbody dorsal scale rows found in European and Chinese mountain '*ursinii* s. l.', and 21 scale rows in the rest. Here a similar scale row reduction has taken place independently in two geographically distant areas, a clear case of parallelism. Several other traits can be suspected to have originated in a similar way, e.g. white bellies and small size that characterise several mountain populations. Such character states must be considered as homoplasies or plesiomorphics, with a low phylogenetic value content.

The test is to see whether mountain populations are more closely related to nearby lowland populations than to other, geographically more distant but phenetically similar mountain populations. If this is the situation, different lowland populations may appear similar through phenetic characters with the same character states.

Table 43. List of taxa and derived character states used in the cladistic analysis in the *Vipera ursinii* s. l. complex

4.	Mean number of preventrals more than two	*renardi* (west), *renardi* (east), *lotievi*, *tienshanica, parursinii*, 'Altai form of *renardi*'
5a.	Mean number of ventrals less than 130	*ursinii* (France), *ursinii* (Italy), *macrops, graeca, ebneri, anatolica, rakosiensis*
5b.	Mean number of ventrals more than 143	*renardi* (east),*renardi* (west), 'Altai form of *renardi*', *lotievi*
9.	Mean number of posterior dorsal scale rows 16 or less	*macrops, graeca*
11.	Rostral higher than wide	*eriwanensis, ebneri, lotievi, anatolica*
14.	Supralabials normally eight or less	*rakosiensis, ursinii* (France), *ursinii* (Italy), *macrops, graeca*
15.	Sublabials less than ten	*rakosiensis, ursinii* (France), *ursinii* (Italy), *moldavica, macrops, graeca, parursinii*, 'Altai form of *renardi*'
16.	Mean number of circumoculars more than 19*	*renardi* (east), *tienshanica, parursinii*, 'Altai form of *renardi*'
17.	Mean number of loreals less than eight*	*rakosiensis, ursinii* (France), *ursinii* (Italy), *macrops, graeca*
18.	Normally four second chinshields	*eriwanensis, ebneri, parursinii*, 'Altai form of *renardi*'
21.	More than 12 crown scales	*eriwanensis, anatolica, tienshanica, parursinii*, 'Altai form of *renardi*'
23.	Occurrence of divided frontal	*ursinii* (Italy), *moldavica, macrops, graeca, eriwanensis, ebneri, lotievi, renardi* (west), *renardi* (east), 'Altai form of *renardi*', *tienshanica*
25.	Nasal without upper split	*tienshanica, parursinii, renardi* (east), 'Altai form of *renardi*'
36.	Dorsal pattern with a high number of windings (X>60)	*eriwanensis, lotievi*, 'Altai form of *renardi*'
42.	Head concave	*renardi* (west), *renardi* (east), *eriwanensis, ebneri, lotievi, anatolica, tienshanica, parursinii*, 'Altai form of *renardi*'

*= Sum of right and left side

Table 44. Number of characters analyzed and their states, used in the phylogenetic analyses of the *Vipera ursinii* complex. In the analysis 15 morphological characters are used (see text and Table 45)

No.	Character	Character states	Character coding
*4.	Mean number of preventrals	two or less	0
		more than two	1
*5a.	Number of ventrals	medium	0
		very few	1
*5b.	Number of ventrals	very numerous	1
		medium	0
*9.	Posterior dorsal scale rows	17	0
		16 or less	1
*11.	Shape of the rostral	as wide as high	0
		higher than wide	1
*14.	Supralabials	eight	0
		less than 8	1
*15.	Sublabials	ten	0
		nine or less	1
*16.	Circumoculars	few	0
		many	1
*17.	No. of loreals	many	0
		few	1
*18.	Number of second chinshields	in most specimens more than four	0
		normally four	1
*21.	Crown scales	fever	0
		more	1
*23.	Occurrence of divided frontal	yes	1
		no	0
*25.	Nasal with upper split	yes	0
		no	1
*36.	Dorsal pattern	medium number of windings	0
		high number of windings	1
*42.	Shape of dorsal side of head	flat	0
		concave	1

Table 45. Data matrix for the cladistic analysis of the taxa in the *Vipera ursinii* complex. Characters constant within a group, or autapomorphies, were not included in the analysis. Character (N=15)

	Character number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Taxa	4	5a	5b	9	11	14	15	16	17	18	21	23	25	36	42
V. berus	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0
V. u. rakosiensis	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0
V. ursinii (France)	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0
V. ursinii (Italy)	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0
V. u. moldavica	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
V. u. macrops	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0
V. u. graeca	0	1	0	1	0	1	1	0	1	0	0	1	0	0	0
V. anatolica	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1
V. eriwanensis	0	0	0	0	1	0	0	0	0	1	1	1	0	1	1
V. ebneri	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1
V. lotievi	1	0	1	0	1	0	0	0	0	0	0	1	0	1	1
V. renardi (west)	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1
V. renardi (east)	1	0	1	0	0	0	0	1	0	0	0	1	1	0	1
V. renardi (Altai)	1	0	1	0	0	0	1	1	0	1	1	1	1	1	1
V. r. tienshanica	1	0	0	0	0	0	0	1	0	0	1	1	1	0	1
V. r. parursinii	1	0	0	0	0	0	1	1	0	1	1	0	1	0	1

Evaluation of characters

Vipera ursinii s. l., seems to be well adapted for burrowing down into the thick and dense grass layer in their typical meadow/steppe habitats. As indicated elsewhere, compact head scalation such as low numbers of scales on snout, as well as unification of head plates, can originally be a result of selection for burrowing/pressing behaviour. In addition, the markedly enlarged rostral in different taxa, as well as the shape of the dorsal side of snout, with somewhat raised canthus rostralis in other taxa might well be results of similar selection.

Low numbers of certain scale characteristics, such as ventral and subcaudal numbers and number of labials and dorsal scale rows have currently been interpreted as primitive states of characters in *Vipera* (e.g. KRAMER 1961, SAINT GIRONS 1978). However, low numbers below, what is generally occurring in related groups of snakes, have also been considered as apomorphic states in the same way as very high numbers of these characters, e.g. MARX and RABB (1970, 1972).

These authors regarded the low number of ventrals found in *V. ursinii* s. l. as an apomorphic state.

The most frequently occurring state in different types of characters is normally considered as a plesiomorphy. Nine dorsal head shields is the most frequent state within Caenophidia. Species or groups with more than nine shields (e.g. shields more fragmented) as well as taxa with fewer than nine shields (shields secondary united) are considered as more derived (MARX & RABB 1970). Thus, an increasing degree of fragmentation of the dorsal head shields should be considered as increasing apomorphy. However, fragmentation of certain scales can be a secondary effect of temperature (FOX *et al.* 1961) and carefulness is necessary when selecting characters and states that are supposed to reflect the phylogenetic history. In addition, consequences of special adaptation, e.g. for burrowing behaviour, might cause adaptations in other directions. Furthermore, as stated above (Methods section) parallel biochemical studies have demonstrated a number of parallel or convergent adaptations to similar environments in this complex. At distinct species and subgenus levels, these kinds of adaptations are useful tools in evolutionary studies.

MARX and RABB (op. cit.) take the genus *Vipera* s. l. as an example and state that *V. berus* has the most plesiomorphic state by e.g. retaining large paired parietals. *Vipera ursinii* s. l. was considered more derived in this character as the parietals were fragmented into smaller scales in their material. However, there is considerable variation in this character between different populations, where *rakosiensis* normally has unfragmented parietals while alpine populations have a varying degree of fragmentation. Thus the mountain populations of *V. ursinii* s. l. should be more derived in this character than the lowland *rakosiensis*. The normal state of dorsal head shields is nine and derivations below or above that number could be opposing apomorphic trends.

A similar argumentation can be applied for many other standardised scale patterns. MARX and RABB (1972) considered it for the number of ventrals as discussed earlier, and this can also be stated for the number of supralabials. Especially as it is in concordance with a series of other character states in scalation of the *Vipera ursinii* complex and it can be considered apomorphic (fulfils the third criteria for derivativeness "=correlation of derived states" of MARX and RABB 1972). The taxon *ursinii* and *rakosiensis* has in general eight supralabials while the *renardi* group has nine. It is generally believed that the original state was eight and the derived state nine (SAINT GIRONS 1980, consider *renardi* as younger then *ursinii*). Alternatively, were nine supralabials the original state (as MÉHELY 1911, believed) and a reduction to eight is an apomorphy? The normal state in Viperidae and in Caenophidia in general is around eight to nine. Increasing numbers of

supralabials in *Vipera*, e.g. ten supralabials in northern *V. xanthina*, has earlier been considered as an apomorphic state (NILSON & ANDRÉN 1986). Thus, we also believe that a much-reduced number must be considered as an apomorphic state in opposed direction. Such a trend is verified by the state in *graeca* and to some extent in *macrops* with occasionally only six supralabials. The low number is a secondary union of young origin and thus clearly an apomorphic state. In mountain dwelling European *V. ursinii*, s. l. supralabial sutures are characterised by a dark-edged pattern. In some examined specimens of *macrops* with only six, and in one case only five supralabials, the dark-edge pattern from the six or seven original supralabials still persist (NILSON & ANDRÉN 1987). Thus the evolutionary trend in reduction of number of supralabials from nine in *renardi*, eight in *rakosiensis* and *ursinii*, around seven in *macrops* and to the very low value of six in *graeca*, seems to be an apomorphic line. In the related forms (*berus, seoanei, bosniensis, nikolskii*, and *barani* – and in *kaznakovi* (which like *seoanei* may have branched off from the *aspis* lineage (HERRMANN *et al.* 1987, 1992, HERRMANN & JOGER 1997)) – the most frequent state is nine supralabials. Six supralabials are rare in the entire Caenophidia and do not occur elsewhere in Viperidae (except in *Adenorhinos barbouri*, another terrestrial/fossorial viper), and thus fulfil all criteria of apomorphy, as is also the case for the characters discussed earlier.

Unique characters for *V. ursinii* s. l. are the enlarged upper preocular, which reaches the nasal, and the single apical plate. A discussion whether or not *V. ursinii* s. l. is a "primitive" taxon can not be done without evaluating their degree of derivativeness. An outgroup comparison with Colubridae or with any other viperine snake shows that these are unique characters and which only rarely occur in other (mainly tropical) Colubroidean species.

The normal state among colubrids is two apicals in contact with rostral as is also the case in *V. berus*, and therefore this state here is considered as the most original state within *Vipera*. Increased numbers of apicals (fragmentation) as well as the occurrence of a single one (secondarily united) are here considered as opposed evolutionary trends. The last state is a synapomorphy for the *Vipera ursinii* complex as a whole, although not always the situation amongst all individuals.

The same argumentation is applied to the large upper preocular that is in contact with the nasal, and which should be looked upon as a derived state. In the European subalpine *ursinii*, the lower preocular is also enlarged and often reaches the nasal below the upper preocular. Thus, the European alpine taxa have a reduced number of loreals, which is also considered as an apomorphic trend. Thereby "*Vipera ursinii* s. l." is not the most original or "primitive taxon" within genus *Vipera*, but instead a derived opposed lineage compared to other members of the genus, a fact also verified by immunological studies (HERRMANN *et al.* 1987, 1992).

Obviously, *Vipera ursinii* s. l. shows a strong (apomorphic) reduction of cephalic scalation, and in particular on the snout. This pattern has evolved a number of times in more or less fossorial species. One such convergence as mentioned above is the low number of supralabials found in *Vipera ursinii* s. l. and in the terrestrial-fossorial African viperine *Adenorhinus barbouri*. Also the enlarged nasal plates found in *graeca* and the single apical and enlarged preoculars can be explained by selection for a fossorial habit. In fact, *Vipera ursinii* s. l. is to a very high extent a species with a subterranean habit. It is mainly restricted to meadow and steppe habitats and it often escapes straight down into the grass and soil cavities when disturbed. Other vipers normally occur close to terrestrial hiding-places, such as stonewalls, stonepiles, boulders, tussocks, hedges etc. Only *Vipera ursinii* s. l. (and the members of the *V. kaznakovi* complex, which has similar snout adaptations) prefers to escape down vertically or into dense tussocks when disturbed. Consequently, we believe that also other snout scalation characteristics have been submitted to the same selective pressure, resulting in unification, low numbers and big sizes of snout scales. We consider these 'reduction' stages of snout scalation as apomorphic states within this complex.

The degree of dorsal scale reduction varies extensively between different populations. The midbody scale row number has consistently been used as an important character separating mainly eastern and western populations. However, the midbody scale count is only a spot check and does not tell us anything about the level of scale reduction along the body. In the eastern lowland populations (=*renardi* and associated populations) the level of dorsal scale reduction from 21 to 19 dorsal scale rows is usually situated on the last third of the body, which results in 21 midbody scale rows. In the western lowland populations (*rakosiensis*) the level of reduction from 21 to 19 scale rows is on the first third of the body, which in turn most often results in 19 midbody scale rows. In the geographically and morphologically intermediate *moldavica* in Romania (Danube Delta and Moldavia) (Figs 5, 7) the reduction can occur all along the body with a varying mid-dorsal scale row number as a consequence. All these populations also have 21 dorsal scale rows on neck (one head length posterior to head).

On the contrary all the European and Chinese mountain populations have 19 dorsal scale rows on neck. In these snakes, the reduction from 21 to 19 scale rows takes place immediately behind the head (see Fig. 5, Tables 16 and 17). The Middle East subalpine populations in Iran and Armenia have normally 21 dorsal midbody scale rows as the scale reduction in these populations is also behind the midbody. In subalpine populations there seems to be a strong selective force for a reduction of dorsal scale rows as the reduction zone moves forward in such small specimens. Perhaps this is in concordance with size reduction as all these mountain taxa consist of small specimens.

The level of reduction varies, however, between different subalpine populations and in some, such as *eriwanensis* and *ebneri*, the reduction site has not moved forward to a similar extent.

All characters are numeric and gradual, except the shape of the rostral (character 11) and the shape of the head (character 42). The quantitative multistate characters are somewhat difficult to delimit in order to get the polarisation states. All these multistate characters are given equal weight. The two qualitative binary shape characteristics mentioned above are given double weight.

Phylogenetic relationship within the Vipera ursinii *complex*

The branch and bound algorithm, using PAUP, is based on discrete characters (N=15) with presumed phylogenetic contents. This procedure gave 10 equally parsimonious cladograms (each of 33 steps and a CI of 0.51 (Fig. 15)). Using selected characters with presumed phylogenetic informative contents a phylogeny could be constructed, that has some similarities with the molecular-based phylogeny obtained in earlier studies (JOGER *et al.* 1992, NILSON *et al.* 1993).

Arrangement of a strict consensus tree and a majority rule tree did not differ otherwise than that *lotievi* is separated from the other three Middle East taxa (Fig. 15). The European group is separated in a clade of its own and *renardi* and the Asian taxa form a second clade.

Thus, in the Asian clade there is a separation of the west-*renardi* and the others, which, to some extent, reflects the geographical connections and their supposed relationship to western and eastern mountain taxa. The west *renardi* forms a sistergroup to the West Asian Mountain taxa. This clade consists of *lotievi, anatolica, eriwanensis* and *ebneri*, and the last three form an unresolved trichotomy. In the strict consensus, *lotievi* was also included in this trichotomy. The east-*renardi* is a sister group to a clade consisting of the eastern mountainous *tienshanica* and *parursinii*, and the lowland 'Altai form of *renardi*'. In all cases (and the consensus tree) *parursinii* and the lowland *renardi* forms a clade, with *tienshanica* in the base as a sister taxon.

In the European clade, the Balkan *macrops* and *graeca* form a separate clade, while *rakosiensis* and French *ursinii* form a second. Together with Italian *ursinii*, they form another unresolved trichotomy. *V. u. moldavica* is clustered at the base of this European clade.

The difference from earlier molecular analyses is the position of *moldavica*, which here is connected at the base of this European clade. In this European clade, the Balkan populations *macrops* and *graeca* form a separate clade and French *ursinii* and *rakosiensis* a second, and with Italian *ursinii* as a sister group to both clades. This creates a problem as the two (Italian and French) *ursinii* samples

phylogenetically could be looked upon as separated taxa, being separated terminal ends in this phylogenetic reconstruction. However, in their electrophoretic profile of serum albumin (Fig. 67) they are identical, in contrast to *rakosiensis*, and to *macrops* and *graeca*, which all are well separated from each other and from the two *ursinii*. Being aware of this dilemma we tentatively place the two *ursinii* groups in the same taxon; *Vipera ursinii ursinii* s. str. On the other hand, the lowland *rakosiensis*, which is clustered together with French *ursinii* is treated as a good taxon for the same reason (besides molecular reasons, also phenetic characteristics not included in this phylogenetic reconstruction, habitat, reproduction etc.).

Genetically *moldavica* is close to *macrops*, while *rakosiensis* seems to be near *ursinii* (see below). In this phylogenetic reconstruction based on morphology,

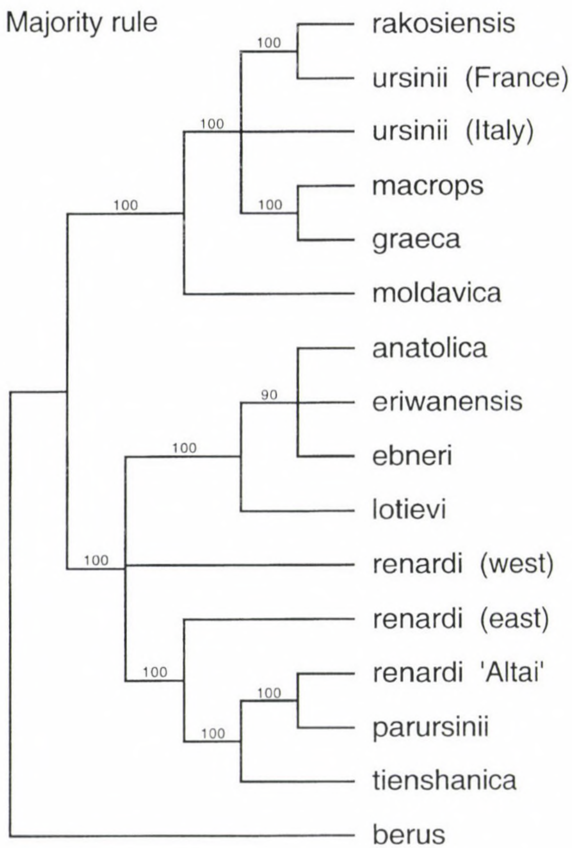


Fig. 15. Phylogenetic hypotheses for the *Vipera ursinii* complex generated with PAUP using the Branch and Bound algorithm on 15 discrete characters (see text). PAUP identified 10 trees with 34 steps. Majority rule consensus tree

the same pattern was not achieved, but the tree is not contradictory to these earlier results.

In character 9 ('number of posterior scale rows') *moldavica* approaches *macrops* and *graeca* (and Italian *ursinii*) (Tables 14 and 15) in having a lower number of scalerows (here considered as derived).

Additional phylogenies

We have been trying to evaluate the phylogeny in different ways (see Table 4). The phenetic and phylogenetic approaches based on morphometrics (2 and 6) have been discussed above. Not all taxa and populations have been available in the other studies.

However, both the immunological and the electrophoretic studies based on albumins (1 and 5) were concordant in the results with the complex divided into three clades (see Figs 66, 68, redrawn from the concerned papers). These clades are a Balkan clade, including *graeca, macrops* and *moldavica*; a Central European clade including *ursinii* and *rakosiensis*; and an eastern clade gathering *renardi*, *eriwanensis* and *anatolica*. The last two clades are separated from the Balkan clade by at least seven IDUs (Immunological Distance Units), which is a distance equal to that between full species of vipers (HERRMANN *et al.* 1992). A similar distance separates *anatolica* from *renardi* and *eriwanensis*, and *moldavica* from *graeca* and *macrops*. Thus the immunological distances indicate a long time of genetic separation between these groups of populations and strongly suggests that we are dealing with at least five full species: 1, *anatolica*; 2, *renardi* and *eriwanensis*; 3, *ursinii* (including *wettsteini*) and perhaps *rakosiensis*; 4, *graeca* and *macrops*; and 5, *moldavica*. These clades are obviously representing separated evolutionary lineages.

The electrophoretic pattern of albumins (5) strongly support this pattern, with *anatolica, ursinii, graeca* and *moldavica* differing from each other and from all the other investigated ones (west-*renardi* (Ukraine), east-*renardi* (Kazakhstan), *eriwanensis, rakosiensis, macrops*) in their main anodic bands. This is to an extent that is usually found only between different species (Fig. 67). The different *renardi* samples (from west and east) showed intraspecific differences, which is in concordance with differences in scalation characters as stated earlier.

Allozyme electrophoresis (3) was performed for the Caucasian groups of taxa during more comprehensive studies of the vipers of Caucasus. Here only *renardi*, *lotievi* and *eriwanensis* were included (together with different populations of *kaznakovi* and *dinniki*). The allozyme pattern showed great genetic similarity between the alpine *lotievi* and *eriwanensis*, but a larger distance to *renardi*. At the northern edge of Caucasus, *renardi* is parapatric with *lotievi*, albeit occurring in

different habitats (alpine/subalpine meadows versus lowland steppe). These two taxa act like different species in nature, a conclusion supported by the genetic profile.

SYSTEMATICS

Thus a pattern emerges with three branches of *'ursinii'*, consisting of lowland taxa: west- and east-*renardi, moldavica*, and *rakosiensis*, respectively, and series of subalpine or alpine species, or taxa approaching species level. The lowland taxa are ecologically and altitudinally completely separated from the more southerly situated mountain populations. The latter occur on alpine and subalpine meadows as well as in the oromediterranean vegetation belt, at altitudes ranging between 1000 and 2500 m. Specimens in the alpine populations are also morphologically distinct. They are markedly smaller, and with less lateral and dorsal pattern on body and head. The 'Altai form of *renardi*' is a lowland exception, with alpine morphology and rocky habitat preference.

DELY and STOHL (1989*a*) stressed that the ecological stenocoenose is to a high extent a physiological specialisation, which supports our hypothesis of mountain populations having a younger evolutionary history, and with a 'phylogenetic direction' from north towards south (Fig. 16). It is inconsistent with modern phylo-

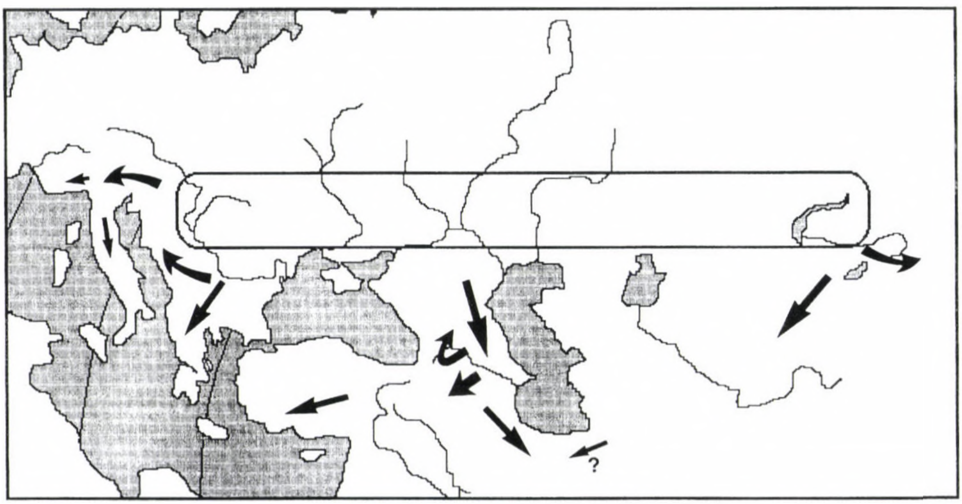


Fig. 16. The hypothetical dispersal routes of the ancestors to the extant mountain populations. Dispersals are mainly south directed. Encircled area shows the distributions of lowland taxa (*rakosiensis, moldavica, renardi*). See text for discussion

genetic and speciation theories that all the hundreds of isolated mountain populations, unique in pholidosis, and ranging from Western Europe to Western China should be the old ancestral form of *'ursinii'*. Moreover, with the wide ranging lowland "puszta" and steppe vipers as younger and more differentiated forms. We reject that traditional hypothesis.

The mountain populations seem to have branched off from the plesiomorphic lowland lineages on a number of different occasions resulting in several geographically separated mountain populations. These are the West European ones; the Balkan ones; the populations in Anatolia, Armenia, Caucasus and Azerbaijan, and finally the ones in Iran, Transcaspian republics of the former USSR and northwestern China. The Asian ones seem to have their origin in ancient forms of the lowland *renardi* populations (perhaps "*ursinoides*" in the sense of NIKOLSKY (1927). NIKOLSKY postulated about a hypothetical ancestor of *'ursinii'* and *sachalinensis* from the beginning of the (last?) glaciation period). The European ones might have evolved from ancestral forms of *rakosiensis* and *moldavica*.

The Caucasian–Transcaucasian group consists of three geographically separated groups of populations of which two, *ebneri* and *eriwanensis*, are geographically rather close, although morphologically different. The *ebneri* populations are found in the mountains of northern Iran and following the Talysh Mountains up into Southeastern Azerbaijan. This taxon has its closest relation towards the northwest (*eriwanensis*), and if considered as a subspecies, it must be of the latter (not of *ursinii* s. l., or of *renardi*). However, we prefer to treat it as an evolutionary species.

The *eriwanensis* populations are distributed in Armenia and on the border mountains into Azerbaijan, which included the whole Sevan lake region, and adjacent Turkey (provinces of Kars and Erzurum). The third taxon in this group, *lotievi*, is restricted to the Great Caucasus and separated from the southern mountain populations by the Kura basin. The Aras river basin separates *eriwanensis* and *ebneri*.

As it seems, the populations in the mountains of Kazakhstan, Kirgizia, Tajikistan and China (*tienshanica* and *parursinii*) have originated from the Kazakhstan lowland *renardi* lineage (=east *renardi*), strongly indicated by several morphometrics.

The Turkish *anatolica* is morphologically derived in many character states. It has gone through a convergence towards the typical mountain-*ursinii* morph, such as an earlier reduction of dorsal scale rows, smaller size, light belly, fewer lateral head scales, reduced number of ventrals and subcaudals, etc. However, it is united with the *renardi–eriwanensis* branch in plesiomorph character states. Such states are many preventrals, many mental rows, more posterior dorsal scale rows, many loreals, many sub- and supralabials, less divided parietals, and broad postorbital

Table 46. Variation, given as mean (X) of selected morphological characters in the alpine populations in Asia and southern Europe (n.b. *lotievi* enters Europe in north Caucasus)

	Posterior scale rows	Supra-labials	Loreals	Sub-labials	Circum oculars	Mentals
			EAST			
V. r. parursinii	17.0	8.8	5.3	9.7	10.0	4.3
V. r. tienshanica	16.9	8.7	4.4	10.4	9.8	3.8
V. ebneri	17.1	9.0	4.0	10.1	8.8	4.9
V. lotievi	17.0	8.6	4.0	10.1	9.1	3.8
V. eriwanensis	17.0	9.0	5.1	10.0	9.3	4.6
V. anatolica	16.8	8.0	4.8	10.5	9.3	4.0
			WEST			
V. u. graeca	15.1	6.3	2.1	8.1	8.4	3.5
V. u. macrops	16.1	7.6	2.5	9.0	8.0	3.5
V. u. ursinii (Italy)	16.5	8.0	3.3	8.9	8.7	3.6
V. u. ursinii (France)	16.9	8.1	3.6	8.8	8.6	4.3

band (covering most of third temporal). But also exhibits characters here treated as apomorphies: high rostral shape, more fragmented crown scales, more circumoculars, white labials, reduced lateral body blotches, etc. All these are character states that separate this Middle East 'subspecies group' of subalpine meadow vipers from its European subalpine equivalents (see also Table 46).

The Middle East 'subspecies group' has its origin back in the *renardi* lineage, and the European and this Middle East subalpine subspecies group are consequently of polyphyletic origin. Furthermore, the Asian ones belong to two separate evolutionary lineages. Thus, *renardi* and its related taxa are treated as a separate evolutionary lineage with *renardi* as a full species. Evolutionarily, none of its descendants can thereby belong to *V. ursinii* s. str., but to *renardi* as subspecies or species of that lineage. Nomenclature changes are therefore inevitable if we consider these as evolutionary lineages.

The West European alpine group, (*ursinii* s. str.), is restricted to the French (formerly as ssp. *wettsteini*) and Italian populations. This is in agreement with DELY and STOHL (1989*a*), who pointed out the round shape of the head, which separates this group from the other European populations. The Balkan group contains the mountain populations in former Yugoslavia and northern Albania (*macrops*), and Greece (*graeca*). On a phylogenetic basis, we consider *macrops* as separated from *ursinii*. DELY and STOHL (1984, 1989*a*) have also taken this position based on analysis of scalation morphology and cranial osteology. The series of European mountain populations shows a phenetic west-east clinal variation in

some characters, with the highest values in the French populations and the lowest ones in Greece. Some mean values are shown in Table 46. The number of posterior dorsal scalerows decreases towards east with 17 in France and 15.1 in Greece. The numbers of supralabials are 8.0 in France and 6.3 in Greece. The number of loreals counted on both sides are 3.5 in France and 2.1 in Greece. This trend in decreasing values towards east contrast sharply against *anatolica* and the other West and Central Asian taxa, which all have higher values in these characteristics. The *eriwanensis* populations have nine supralabials on each side while *anatolica* has eight. This indicates a clinal variation in this character also in this group, although not so pronounced, and on a higher level than in the compared European mountain groups. In the European populations, this clinal variation must be the result of an ecological convergence as the European mountain populations are polyphyletic.

The specimens at the Valea lui David population in Romanian Moldavia belong to *moldavica*, a taxon closest related to the Balkan mountain populations (*macrops*). As discussed below (see under *moldavica*), there might be a case of true sympatry in Moldavia between *moldavica* and *renardi*, and if so verifying the separation of these two taxa at species level (besides the molecular evidence). As shown elsewhere (NILSON *et al.* 1993), *renardi* and *rakosiensis*, and *moldavica* and *rakosiensis*, respectively, are genetically well separated (representing different phylogenetic lineages). *Rakosiensis* is closest to the West European Mountain *ursinii* populations.

Furthermore, *macrops* and *rakosiensis* are well separated from each other, which was verified by osteological studies made by MÉHELY (1911) at the beginning of this century. MÉHELY found considerable differences between these two (his *macrops* and *ursinii*) in cranial osteology. He also found considerable differences between these two taxa and *renardi*. However, *renardi* and *rakosiensis* are more similar to each other than either of them is to *macrops* (MÉHELY 1911, DELY & STOHL 1984, 1989*a*). This is to a certain extent in line with the biochemical results of JOGER *et al.* (1992). In the same way the Almaty population (=*tienshanica*) also differs from *renardi* in cranial osteology (DELY & STOHL 1989*b*).

Based on our earlier studies (JOGER *et al.* 1992, NILSON *et al.* 1993) together with the present one (see discussion above, on phylogenetics) we have five evolutionary lineages in the *Vipera ursinii* complex s.l:

1. lowland *rakosiensis*, mountain *ursinii*;
2. lowland *moldavica*, mountain *macrops* and *graeca*;
3. lowland (west)*renardi*, mountain *eriwanensis*, *ebneri*, and *lotievi*;
4. lowland (east)*renardi, tienshanica*, the 'Altai form of *renardi*' and *parursinii*;
5. mountain *anatolica*.

In the absence of fresh material or tissues, no molecular studies have been carried out for the eastern populations. Therefore, we have not been able to demonstrate the origin and relations in all cases.

Below we list the different taxa that we recognise. Some of the taxa have earlier in the literature been treated as subspecies or been placed as synonyms with others. However, the taxa recognised here are those evolutionary lineages we that can identify based on phylogeny, zoogeography and ecology.

Groups of populations are geographical entities. We consider that full speciation events have occurred in several of the examined taxa, and thus being full, albeit cryptic species in a phylogenetic perspective, although not always following the 'biological species concept' (BSC). BSC is based on reproductive isolation, a fact that would reduce the total number of species of vipers in the genus *Vipera* s. l. from perhaps about 25 evolutionary species to about six biological species! (Comparable with situation in plethodontid salamanders, ARNOLD *et al.* 1993, LARSON & CHIPPINDALE 1993). Neither would there be more than one, two or three species in the *ursinii* complex in a 'phenetic species concept'. Exclusive confidence in the demonstrated phenetic similarities (as exemplified by the demonstrated convergence between various mountain populations of *ursinii* s. l.) would lead students of phenetics to continuously unite such taxa (NILSON 1998).

We believe in a series of full phylogenetic species, albeit cryptic in several cases. This sibling species level has not been possible to demonstrate by genetics in all cases, and the taxonomic position is demonstrated here by placing the traditional species name in apostrophs. One effect is that *renardi* is paraphyletic, unless we separate the eastern and the western *renardi* in two species. In such a scenario, the western *renardi* lineage will constitute of a series of sister taxa: *Vipera renardi, V. lotievi, V. eriwanensis, V. ebneri* and *V. anatolica*. The eastern *renardi* lineage would be represented by a polymorphic taxon divided into a series of subspecies: *Vipera 'r. renardi', V. 'r' tienshanica'*, 'Altai form of *renardi*' and *V. 'r'. parursinii.* We have not executed this taxonomic division here as there was not enough phylogenetic information available for the eastern populations. Nevertheless, we believe that future studies of these groups will point in this direction.

We have neither separated the European taxa on species level, partly because it was not supported by the Multivariate Analyses.

TAXONOMIC ACCOUNT

Vipera 'ursinii' ursinii (BONAPARTE, 1835)
"Italian/French meadow viper"
(Fig. 17)

Pelias ursinii BONAPARTE 1835, Icon. Fauna Italica Anim. Vert. 2 (12), 65 pp. (pl.). – Terra typica: Italy, Abruzzen, "close to province Ascoli". Holotype: Academy of Natural Sciences of Philadelphia (ANSP) No. 6915. This specimen was designated as lectotype by KRAMER (1961), but Bonaparte described the taxon on a single specimen, certainly ANSP 6915 (MCDIARMID *et al.* 1999), which outruns lectotype designation. Leg. BONAPARTE (1835). See MCDIARMID *et al.* 1999, p. 411–412 for further discussion about type and original publication.

Vipera ursinii, BOULENGER 1893a (part.), Proc. Zool. Soc., London 1893: 596–599 (pl. 51).

Vipera ursinii ursinii, L. MÜLLER, In STEINHEIL 1927, Europas Schlangen 7/9: 31–45 (pl. 34).

Vipera ursinii wettsteini KNOEPPFLER & SOCHUREK 1955, Terra typica: Montagne de Lure, Basses Alps. Holotype: Naturhistorisches Museum Wien, No. 14990. Leg. KNOEPPFLER & SOCHUREK 1955.

Description. It is a small to medium-sized taxon. Maximum total length in our material is 40.8 cm for males (of which tail length is 4.6 cm), and 43.7 cm for females (tail 4.0 cm).

Head and body pattern present, but somewhat reduced laterally. Belly-pattern whitish. Dark spots on cheek, on labials and on lateral and dorsal sides of head including narrow occipital and postorbital stripes; lateral sides of body light with blotches or spots present (may be weakly developed in some specimens); dorsal pattern consists of a band with rounded corners of windings.

Posterior supralabials more equal to anterior ones in size, 7 to 9 supralabials on each side and with the fourth under orbit. One to six loreals. Nasal mostly normal, but with a upper nasal split; upper preocular normally in contact with nasal; parietals divided.

An early reduction of dorsal scale rows (from 21 to 19 rows at the position between the fourth and the 14th ventral) i.e. 19 dorsal scale rows on neck and at midbody, and 17 anterior to anal plate. Low number of ventrals. Medium number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values (±S.E.) for 65 specimens of both sexes are as follows: preventrals: 1.52±0.11 (1.66±0.14 for the French populations; 1.37±0.16 for the Italian); ventrals: 124.86±0.38 (125.06±0.57 for the French populations, 124.62±0.50 for the Italian); scale rows on neck: 19.26±0.08 (19.49±0.14 for the French populations; 19.00 ±0.00 for the Italian); scale rows on midbody: 18.98±0.02 (18.97±0.03 for the French populations, 19.00±0.00 for the Italian); posterior

→

Figs 17–24. 17–20, 22–23 = Live *Vipera ursinii* specimens: 17 = *V. u. ursinii* from Abruzzi, Italy (Triet collection); 18 = *V. u. macrops* from Korita, Bosnia-Herzegovina (topotypic specimen); 19 = *V. u. graeca* from Pindos Mountains, Greece (paratype); 20 = same, juvenile; 22 = *V. u. rakosiensis* from Dabas, south of Budapest, Hungary; 23 = aberrant female *V. 'u.' rakosiensis*, found by the SEH: Conservation Committee south of Budapest in 1987. She was kept in captivity (JANISCH, Budapest) over the summer and gave birth of nineteen young, and of which three fourths (13) had the same unusual colour pattern as the female. The female and her young were all released at the collecting site in early autumn the same year (JANISCH 1993, KORSÓS, pers. comm.). 21, 24 = Habitat of *V. ursinii*: 21 = *V. u. graeca* at Pindos Mountains, Greece, 2000 m altitude; 24 = *V. u. rakosiensis* at Bugac-Puszta, south of Budapest, Hungary


17


18


19


20


21


22


23


24

scale rows: 16.72±0.08 (16.91 ±0.05 for the French populations, 16.48 ±0.15 for the Italian) ; level of scale row reduction from 21 to 19 rows (at ventral number): 7.74±0.34 (8.63 ±0.48 and 6.94±0.37 for the French populations, 6.70±0.40 and 5.52 ±0.34 for the Italian respectively (at ventral number, and in%)); supralabials (sum of both sides): 16.08±0.09 (16.20±0.14 for the French populations, 15.93±0.08 for the Italian); sublabials (sum of both sides): 17.67±0.14 (17.63±0.21 for the French populations, 17.72±0.18 for the Italian); circumoculars (sum of both sides): 17.32±0.13 (17.23±0.15 for the French populations, 17.43±0.23 for the Italian); loreals (sum of both sides): 6.97±0.30 (7.32±0.40 for the French populations, 6.59±0.47 for the Italian) ; crown scales (intercanthals and intersupraoculars): 11.32±0.32 (11.66±0.49 for the French populations, 10.93±0.38 for the Italian) ; dorsal windings/blotches: 53.42±0.48 (54.51±0.59 for the French populations, 52.10±0.71 for the Italian).

In addition, it is a taxon of the *Vipera ursinii* complex characterized by a unique serum albumin (JOGER *et al.* 1992, NILSON *et al.* 1993). In serum albumin profile, it is most similar to *rakosiensis* together with which it forms an evolutionary lineage of common ancestry, also indicated by immunological results.

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size

3. Non-bilineate body ground colour pattern

4. White belly

5. Lateral blotches and spots on body present (but may be only weakly visible in some specimens)

6. Dark spots on labials and lateral and dorsal sides of head including narrow occipital and postorbital stripes

7. Dorsal zigzag band with rounded corners of windings

8. Variable number of dorsal windings

9. Nasal normally undivided, but with a upper nasal slit

10. Rostral as high as broad

11. A low loreal number

12. Few circumoculars

13. Upper preocular often in contact with nasal

14. Medium number of crown scales

15. More fragmented parietals

16. Few supralabials

17. The three first supralabials of similar size as the following ones

18. Forth supralabial below orbit

19. Few sublabials

20. Few mental scales

21. Early dorsal scale row reduction: 19 rows on anterior part of body and midbody

22. A low ventral number

23. No exposed intersquamose area
24. Medium number of subcaudals
25. Being subalpine/alpine

The Italian and French samples of *ursinii* are rather similar and differs significantly only in the number of gulars (p=0.0004; Fisher's Post Hoc test (PLSD)) where the Italian sample (N=30) has a mean value of 3.63±0.12 S.E, and the French sample (N=35) has 4.29±0.20 S.E. Further, they also differ in the number of anterior scale rows (p=0.0031), the Italian sample has a mean value of 19.0±0.13 S.E. and the French 19.5±0.14 S.E., and also in posterior scale rows (p=0.0013), the Italian sample has a mean value of 16.5±0.15 S.E. and the French 16.9±0.05 S.E.

External morphology evolved as typical for alpine taxa of the *ursinii* complex; similar to *macrops* and *graeca* in various characters, but differs from both in combination of characters (posterior dorsal scale rows, supralabialia shape and numbers, fragmentation of frontal, shape of dorsal band). Differs from lowland *rakosiensis* and *moldavica* by its smaller size, white belly, earlier dorsal scale row reduction, absence of black exposed intersquamose area, no bilineate ground colour, reduced postorbital band. It differs from lowland *renardi* and all Asian mountain taxa (except the Chinese *parursinii*) by having 19 midbody scale rows.

The morphological description of *V. u. ursinii* by SAINT GIRONS (1978) is based on populations here separated as *ursinii*, *macrops* and *anatolica*.

Karyotype of French *Vipera 'ursinii' ursinii* is 2N=36 (14 V+2 I + 20m) (SAINT GIRONS 1977).

Distribution (Fig. 69). *Italy:* It is known from five different areas in Central Italy – the uplands of the Central Appennines, the regions of Marche, Umbria and Abruzzo (terra typica). BRUNO and MAZZEI (1987) figures 12 different populations in this region. CAPULA and LUISELLI (1992) are of the opinion that the taxon is restricted to the three Central Appenninian massifs: Sibillini, Gran Sasso and Velino.

France: Up to 17 different local populations are recognised (BARON pers. inf.). It is reported from Southeastern France – southern uplands of Vaucluse (Ventoux), Haute-Province (Basses-Alpes and areas of de Bayons, de Turriers, montagne de Lure, regions of Castellane), Alpes-Maritimes (montagnes de Cherion, de l'Audibergue, plateaux de Caussols, de Calern) (BARON 1987, BARON *et al.* 1993). The range in France is also discussed by CASTANET (1987).

Habitat. The localities know in France are between 1100 and 2400 m altitude and the habitat consists of south-facing slopes with subalpine meadows, rocks and forests at the tree line. Dwarf Juniper scrubs are frequent in the habitat. Much of the habitat has been altered due to constructions of ski facilities and mechanical

creation of pists. On Mont Ventoux two-thirds of the habitat have been destroyed in favour of winter sports (CORBETT 1989, STUMPEL *et al.* 1992). In Italy, the habitat seems to be of the same type at between 1600 and 2200 m altitude (CAPULA &





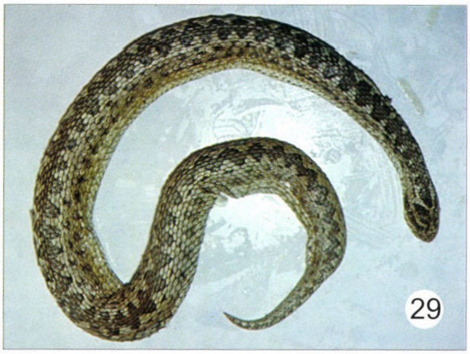














Fig. 27. A female specimen of *Vipera 'ursinii'* cf *moldavica* from Sumen, Kolarovgrad, Bulgaria (Photo Z. TAKÁCS)

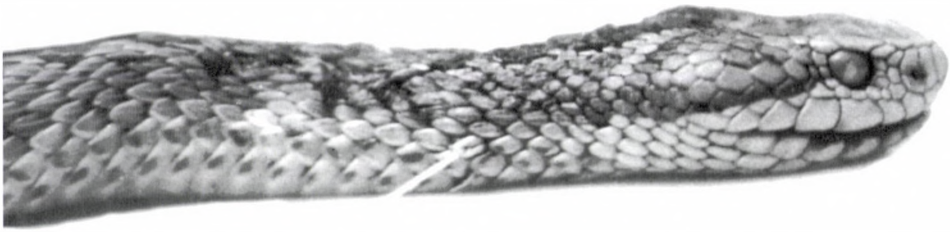


Fig. 28. Lateral view of head of the same female specimen of *Vipera 'ursinii'* cf *moldavica* from Sumen, Kolarovgrad, Bulgaria (Photo Z. TAKÁCS)

LUISELLI 1992). There are different opinions of the real threat in the Italian populations. According to HONEGGER (1981) habitat alterations and destruction are the main threats, while these are not pronounced according to CAPULA and LUISELLI (1992), who stressed the construction of roads and overgrazing by shepherds as more severe threats. Description of habitats can be found in KRAMER (1961) and BRODMANN (1987), with good photographs in the later. The Italian habitat is also discussed by e.g. BRUNO (1967) and BRUNO & MAZZEI (1987).

◄

Figs 25–26, 29–32, 37–38. 25 = Live adult of *Vipera 'ursinii' moldavica:* 25 = female (=holotype) from Valea lui David, Romanian Moldavia (=Terra typica), 26 = male from the Danube Delta population (Photo Z. KORSÓS). 29 = The *'renardi'* morph of *V. 'u.' moldavica* from Valea lui David, Romania, Jasi (specimen from the Natural History Museum collection in Jasi, Romania). 30–31 = The *'rakosiensis'* morph of *V. 'u.' moldavica* from Valea lui David, Romania Jasi (specimens from the Natural History Museum collection in Jasi, Romania) and its habitat at Valea lui David, Romania. 32 = The habitat of *V. 'u.' moldavica* at the Danube Delta, Romania. (Photo Z. KORSÓS). 37 = The habitat of *V. renardi renardi* at central Kazakhstan, 1986. (Photo T. DUJSEBAYEVA). 38 = Adult male of *V. r. renardi* ('east *renardi*') from Tarbagatai Mountains, Kazakhstan (ZIG field no. 212)

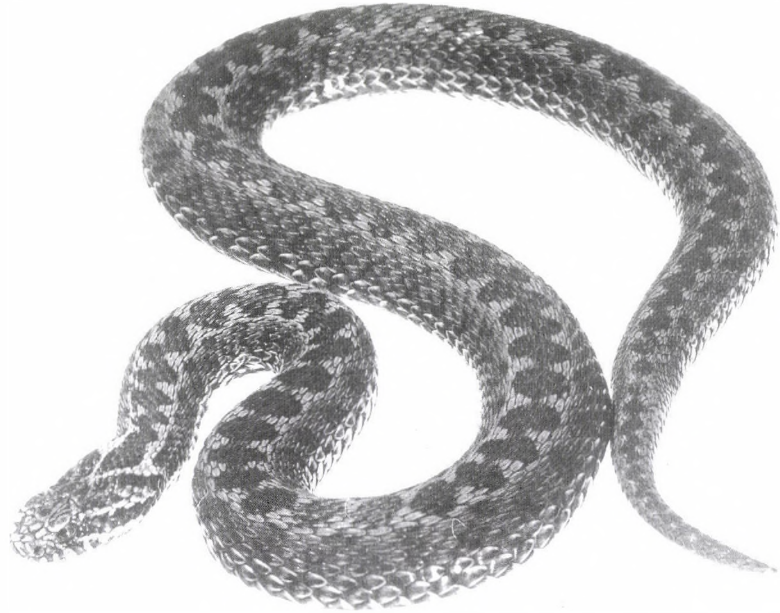


Fig. 33. Adult live female of *V. renardi renardi* ('west *renardi*') from Ukraine (ZIG)

Estimated population size. According to CORBETT (1989), the Italian populations are submitted to a threat that varies from common to highly endangered. According to the SEH Conservation Committee (SEH: CC) it is presently (1997) threatened, but not endangered. We share that opinion. It seems to be reasonably abundant in Gran Sasso and Sibillini areas in Italy (CAPULA & LUISELLI 1992).

The French populations are submitted to a threat that vary from low to highly endangered, and population density can locally be 20 to 30 adult specimens per hectare. The population at Mt. Ventoux is estimated by BARON to be around 1000 adult specimens. According to SEH: CC it is presently (1997) threatened, but not endangered. We share that opinion.

Field observations. We have not had the opportunity to visit the Italian *ursinii* habitats, but French vipers were observed twice, once at Mt. de Lure in the Basses Alps and once at Plateau de Caussols in Alpes Maritimes, Cannes. Of these specimens, only observed in the field and photographed, one semiadult male was found under a stone (Mt. de Lure) near an adult specimen of *Coronella austriaca*. It was after heavy summer rains, and a specimen of *Vipera a. aspis* was basking on

the surface. Three specimens at Caussols, all females, were all basking or moving around in mid June.

Comments. AGRIMI and LUISELLI (1992) studied feeding strategies of the Italian populations and BARON (1992) studied the feeding biology in France. BEA *et al.* (1992) summarises information from both countries.

The intra-subspecific variation in four French populations is thoroughly analysed and discussed by BARON *et al.* (1993). The demography has been extensively studied in the Mont-Ventoux population by BARON *et al.* (1996).

Taxonomic entity. *Vipera ursinii ursinii* s. str. is a well-defined taxon, not close to any other sample examined here. However, it has occasionally been treated as a part of a larger assembly of taxa (as here defined) under the name *Vipera u. ursinii* (s. l.).

Further, it has been divided into an Italian subspecies (*V. u. ursinii*) and a French subspecies (*V. u. wettsteini*), which to some extent can be justified on morphological basis. As such, it has been used as two geographically separated entities in the cladistic analysis. Due to immunological similarity we treat the Italian and French populations as a single taxon.

French and Italian localities, and material examined. FRANCE: Montagne de Lure, Basses Alpes, ca 1400 m (MHNG 1517.28, 1355.31–36, 38. 1592.25, ZIG 140–142, ZIG unregistered, GNM Re. ex. 4925, MNHN 1978.455–6); Lac de Lignins, Basses Alpes (MNHN 1978.457–60); Mourre de Chanier, Basses Alpes (MNHN 1978.398); La Cassine, Basses Alpes, 1300 m (NMHN 1978.399, 1978.425); Turriers, Basses Alpes, 1350 m (NMHN 1978.454); Mont

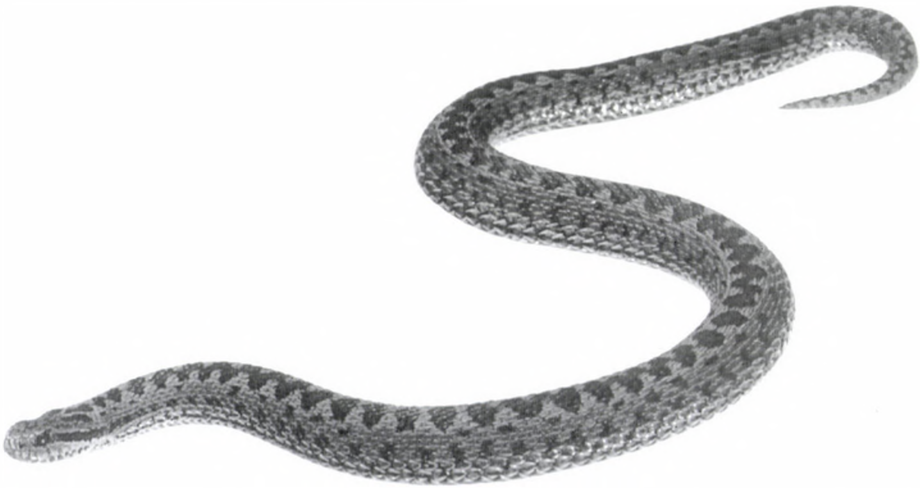


Fig. 34. Adult live female of *V. renardi renardi* ('east *renardi*') from Kazakhstan (ZIG)

Ventoux, département de Vaucluse (MHNG 1355.39, 1404.72, 1592.26, MNHN 1978.400, 8205, A183); "Alpi Marittime" (MZF 12125–6); Coussol, Alpes Maritimes (3 live specimens investigated in the field);

ITALY: Mt. Vettore (ZIG 139); Sibillini (NHMG 1355.1–8, 1354.99–100, MZF 4740, 19495, 19832, 31879–81, 31882, ZIG 252); Mt. Velino (NHMG 1355.9–10); N.E. Rome (NMHN 1966.1064); Gran Sasso (NMHN 1978.439, 1978.441, MZF 31239–40, 31884–6); Mte Cefalone, Abruzzo (MZF 31878); Pizzo di Muscia, Monti della Laga (MZF 31883).

Vipera 'ursinii' macrops MÉHELY, 1911
"Karst viper"
(Fig. 18)

Vipera macrops MÉHELY, 1911, Ann. Hist. Nat. Mus. Hung. Budapest 9: 186–243 (pl. 3, Figs 3–4; pl. 5, Fig. 4) – Terra typica: Korita, Herzegovina, Yugoslavia (restr. MERTENS & MÜLLER 1928).
Lectotype: (KRAMER 1961) Naturhistorisches Museum Wien, No. 7001. Coll. VEITH 1910.
Vipera ursinii macrops, BOLKAY 1924, Mém. serb. Acad., Beograd (Spomenik.). 61(11): 1–29.
Vipera (Pelias) ursinii forma trans. *rudolphi* T. REUSS 1924 (non *Vipera berus rudolphi* T. REUSS 1927 = nomen nudum), Wochenschr. Aquar. Terrar. K. Braunschweig 21: 545–546. – Terra typica: Baba Planina.

Description. It is a small to medium-sized taxon. Maximum total length in our material is 45.4 cm for males (of which tail length is 6.0 cm), and 47.4 cm for females (tail 4.7 cm).

Head and body pattern present, but somewhat reduced laterally. Belly-pattern whitish or mixed white-black or even blackish. Dark spots on labials and on lateral and dorsal sides of head including narrow occipital and postorbital stripes; lateral sides of body light with blotches or spots present (may be weakly developed in some specimens); dorsal pattern consists of a zigzag band, which varies in shape but mainly markedly tagged with pointed corners of windings.

Posterior supralabials markedly smaller in size than anterior ones, six to eight supralabials on each side (occasionally fewer or more), and with the third or fourth under orbit. One to five loreals. Nasal mostly normal, but with an upper nasal split; upper preocular normally in contact with nasal; parietals divided.

An early reduction of dorsal scale rows (from 21 to 19 rows at the position between the second and the tenth ventral) i.e. 21 dorsal scale rows on neck, 19 on anterior part of body and at midbody; 17 or less anterior to anal plate. Low number of ventrals. Medium number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 42–44 specimens of both sexes are as follows: preventrals: 1.91±0.12; ventrals: 127.43±0.58; scale rows on neck: 19.02±0.05; scale rows on midbody: 19.05±0.05; posterior scale rows: 16.14±0.16; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 5.26±0.25 and 4.19±0.20 respectively; supralabials (sum of both sides): supralabials (sum of both sides): 15.26±0.24; sublabials (sum of both sides): 18.02±0.21; circumoculars (sum of both sides): 16.07±0.32; loreals (sum of both sides): 5.02±0.24; crown scales (intercanthals and intersupraoculars): 9.05±0.30; dorsal windings/blotches: 58.58±0.80.

It is a taxon of the *Vipera ursinii* complex characterized by a unique serum albumin (JOGER *et al.* 1992, NILSON *et al.* 1993). By immunological results most similar to *graeca* together with which it forms an evolutionary line of common ancestry.

Diagnosis. Thus a species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size
3. Non-bilineate body ground colour pattern
4. White to black belly
5. Lateral blotches and spots on body present (but may be only weakly visible in some specimens)
6. Dark spots on labials and lateral and dorsal sides of head including narrow occipital and postorbital stripes
7. Dorsal zigzag band with pointed corners of windings
8. Variable number of dorsal windings
9. Nasal normally undivided, but with a upper nasal slit
10. Rostral as high as broad
11. A low loreal number
12. Few circumoculars
13. Upper preocular often in contact with nasal
14. Fewer crown scales
15. More fragmented parietals
16. Few supralabials
17. The three first supralabials larger than the following ones
18. Third or fourth supralabial below orbit
19. Variable number of sublabials
20. Few mental scales
21. Early dorsal scale row reduction: 19 rows on anterior part of body and midbody
22. A low ventral number
23. No exposed intersquamose area
24. Medium number of subcaudals
25. Being subalpine/alpine

External morphology evolved as typical for alpine taxa of the *ursinii* complex; similar to *ursinii* in various characters but unique in combination of characters (posterior dorsal scale rows, supralabialia shape and numbers, fragmentation of frontal, shape of dorsal band). Similar to *graeca* but differs in number of subcaudals, shape of nasal, lateral pattern, number of supralabials). Differs from lowland *rakosiensis* and *moldavica* by its smaller size, white belly, earlier dorsal scale row reduction, absence of black exposed intersquamosal area, no bilineate ground colour, reduced postorbital band. It differs from lowland *renardi* and all Asian mountain taxa (except the Chinese *parursinii*) by having 19 midbody scale rows.

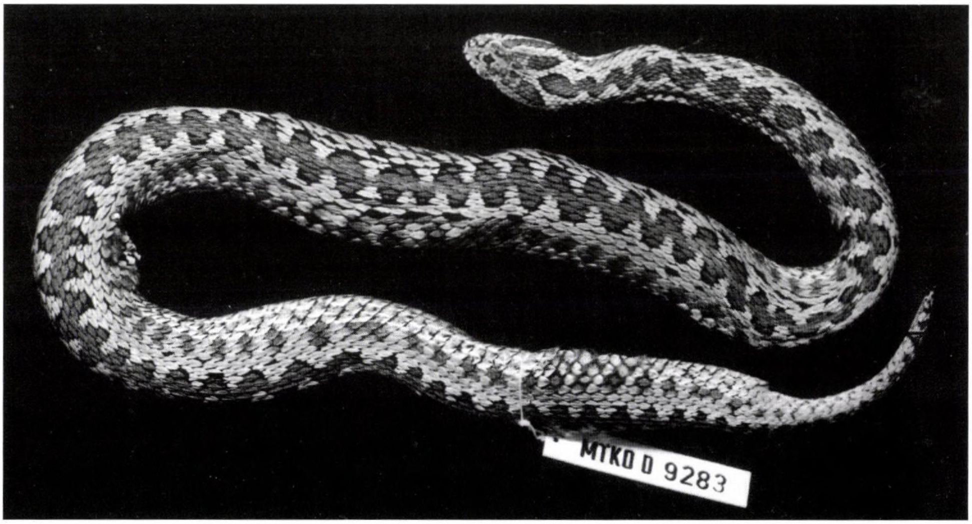


Fig. 35. Adult female of *V. r. renardi* ('east *renardi*') from Dzherzkazgan, Kazakhstan (MTKD D 9283)

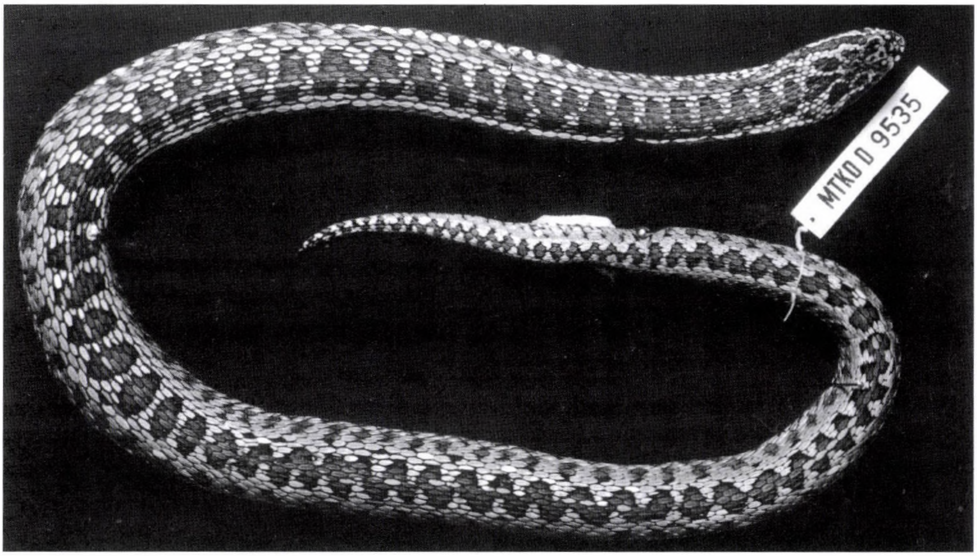


Fig. 36. Adult male of *V. r. renardi* ('east *renardi*') from Dzherzkazgan, Kazakhstan (MTKD D 9535)

Melanistic specimens of *Vipera ursinii* s. l. was never observed during the study, and no proper verification in the literature could be found. Misidentifications of related taxa (*berus, nikolskii, dinniki, kaznakovi*) as being melanistic *ursinii* s.lat. specimens occur frequently, but *macrops* is sometimes pointed out as being melanistic. Examination of available specimens in museum collections, including all in the Vienna Museum did not support this statement. However, partial melanism was observed in Bosnian specimens with the back melanistic and belly and lower parts normal in colour. The same phenomenon, with partial melanism in specimens of *macrops*, was already pointed out by BOULENGER (1913) and VEITH (1991).

Distribution (Fig. 69). This taxon is reported from more than 20 localities on the northern half of the Balkan Peninsula – from the former Yugoslavia (Bosnia, Herzegovina, Montenegro, Macedonia), northern Albania. The population in Lülin-Mountains west of Sofia, Western Bulgaria (BURESCH & ZONKOW 1932, 1934) is here included in *moldavica*.

WERNER (1895, 1897) reported the taxon from the lowland island of Krk, in the Adriatic Sea. This was based on a specimen he had seen in the zoological collection of the Marine Academy in Fiume and which was said to be from "Castelmuschio auf der istrianischen Insel Veglia". KRAMER (1961) also mentions two specimens from that island, which were collected by L-KNOEPPFLER. KRAMER never saw these specimens himself. Also BRUNO (1980) mentions a juvenile specimen that he found at Jezero on Krk. This is the only Krk specimen (MZF 31887) that has been available for us to examine. The range of this taxon on the Balkan Peninsula is further discussed by WERNER (1920), KARAMAN (1928, 1939), RADOVANOVIC (1941, 1964), KRAMER (1961), DIEMOVSKI (1964), POZZI (1966), and SOCHUREK (1984).

Estimated population size. This viper is not well known when it comes to ecology, density and conservation. These populations are probably not highly endangered although rare in many places and rather locally distributed. Locally it is clearly common. According to SEH: CC it is presently (1997) threatened, but not endangered. We share that opinion.

Habitat. Description of habitats can be found in KRAMER (1961) and BRODMANN (1987), with good photographs in the latter. In addition, VEITH (1991) is discussing the habitat. See also 'Field observations' below.

Field observations. One specimen, a male, of *macrops* was observed at Korita, the type locality in Bosnia–Herzegovina, in June 1987. There are comparatively good habitats in this region, and the large number of specimens from this locality in museum collections indicates that the region might have had a high density of this snake. The habitat is hilly, partly deforested mountain meadows, and

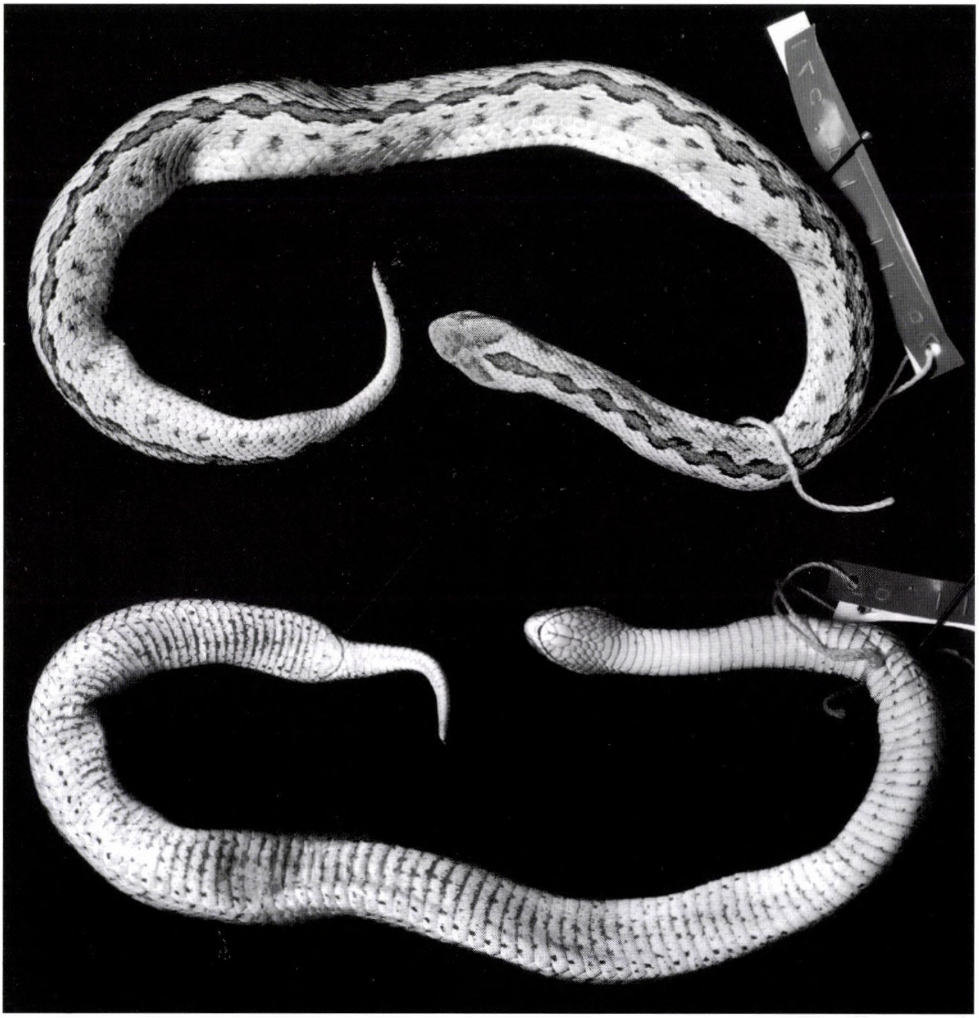


Fig. 40. Male of *Vipera renardi tienshanica* (BMNH 79.11.14.271) from Chinas (Tschinas), Uzbekistan, dorsal and ventral view

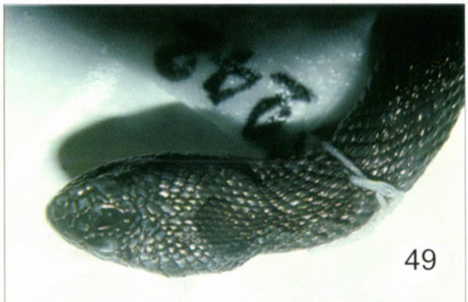
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Figs 39, 41–42, 49, 51–53, 55. 39 = Juvenile male of *V. r. renardi* ('east *renardi*') from Tarbagatai Mountains, Kazakhstan (ZIG). 41–42 = "Tien Shan mountain steppe viper" (*V. r. tienshanica*): 41 = Live female from the foothills of Borohoro Shan, 26 km north on road of Yining Airport, Yining (Gulja (=Kuldja)), Ili Prefecture, Ili Kazak Autonomous Prefecture, Xinjiang, Uygur Autonomous Region, China, at 1030 m altitude, 42 = Habitat at the foothills of Borohoro Shan (Photos T. PAPENFUSS). 49–52 = Head of *V. r. parursinii* ssp. n. (Nilka Xian, Xinjiang): 49 = paratype (CIB 775242), dorsal view, 51 = holotype (CIB 775157), lateral view, 52 = paratype (CIB 775237), lateral view. 53. Adult male of the 'Altai form' of *V. renardi*, from Tagyr, foothills of Altai Mountains, Kazakhstan (ZISP field no. 6314). 55 = Habitat of *V. anatolica*, Ciglikara Ormani (=Terra typica), prov. Antalya, S. Turkey (Taurus Mountains)


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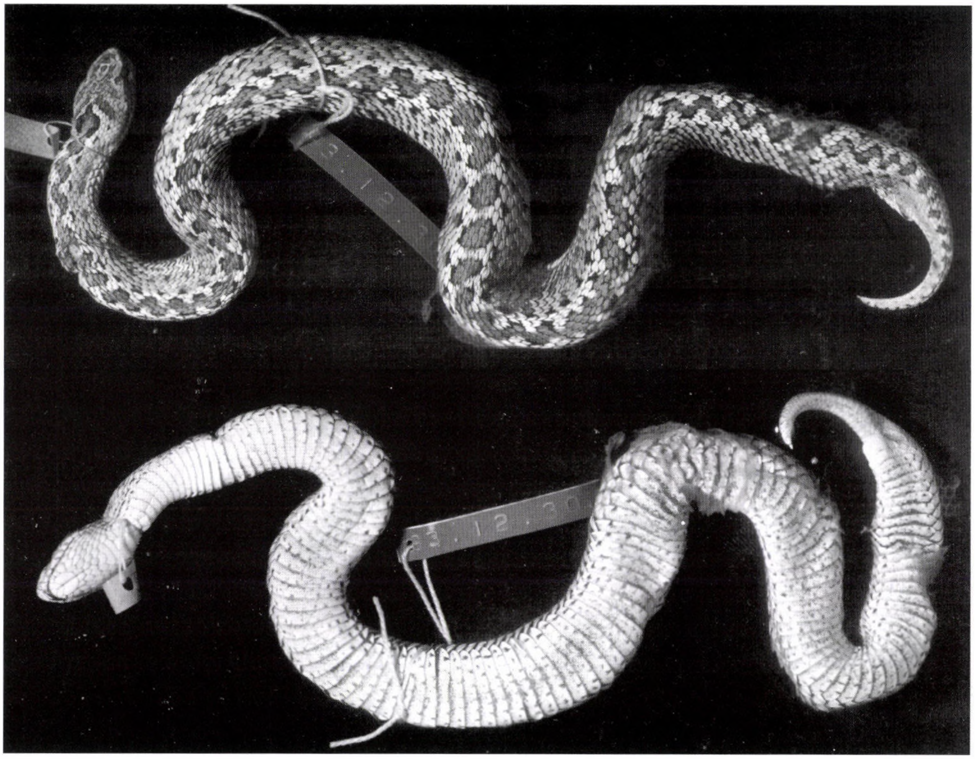


Fig. 43. Female holotype of *V. renardi tienshanica* ssp. n. (BMNH 93.12.30.9) from 'Wernensky Ujesd' (=Almaty), Varnoe, Kazakhstan, dorsal and ventral view

macrops was observed in a small meadow in the low deciduous oak scrub forest. Parts of the meadows also have some smaller karst rocks, and close to the spot where the specimen of *macrops* was found also an adult *Vipera a. ammodytes* was basking on such a rock. *Lacerta agilis bosnica* and *Lacerta t. trilineata* were also observed. In the same region, but in much moister habitat close to a coniferous forest, *Vipera berus bosniensis* was found. *Lacerta oxycephala* was also observed.

Comments. The morphology of this taxon is also discussed by MÉHELY (1911), BOLKAY (1924), SCHWARZ (1936), KRAMER (1961), DELY & STOHL (1984, 1989*a*), VEITH (1991).

Taxonomic entity. *Vipera ursinii macrops* is a well-defined taxon, not close to any other here-examined sample. However, it has occasionally in literature been treated as a part of a larger assembly of taxa (as here defined) under the name *Vipera u. ursinii* (s. l.).

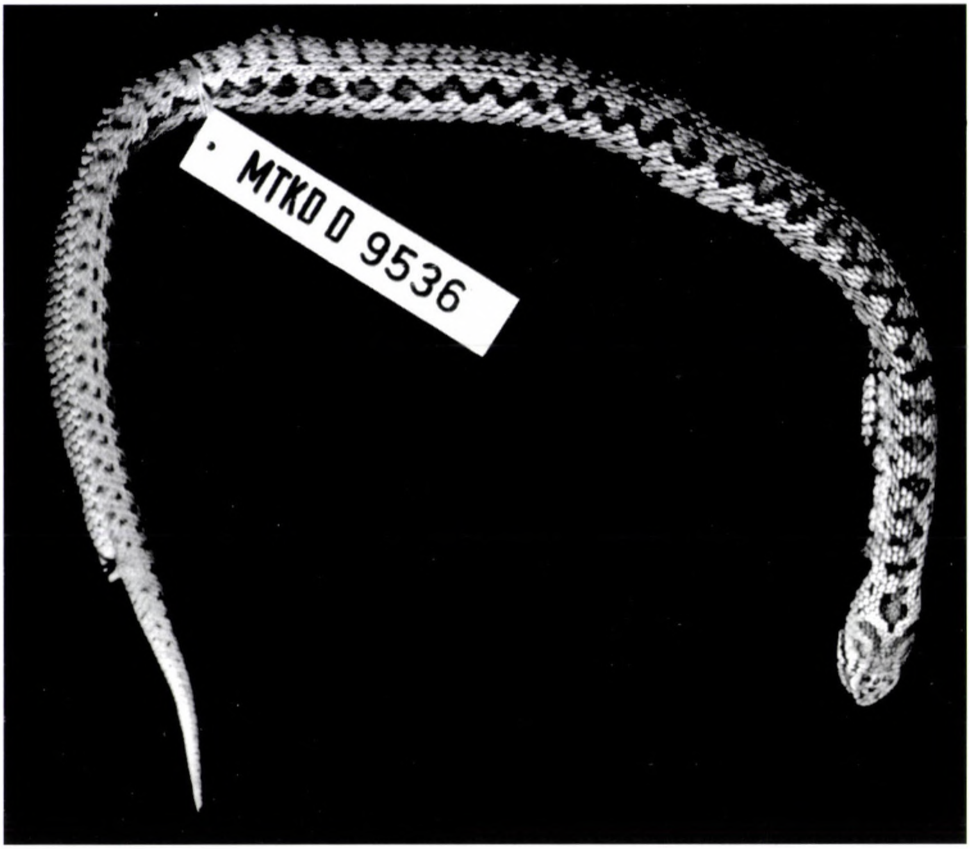


Fig. 44. Male *V. renardi tienshanica* (MTKD D 9536) from Alma-Ata, Kazakhstan

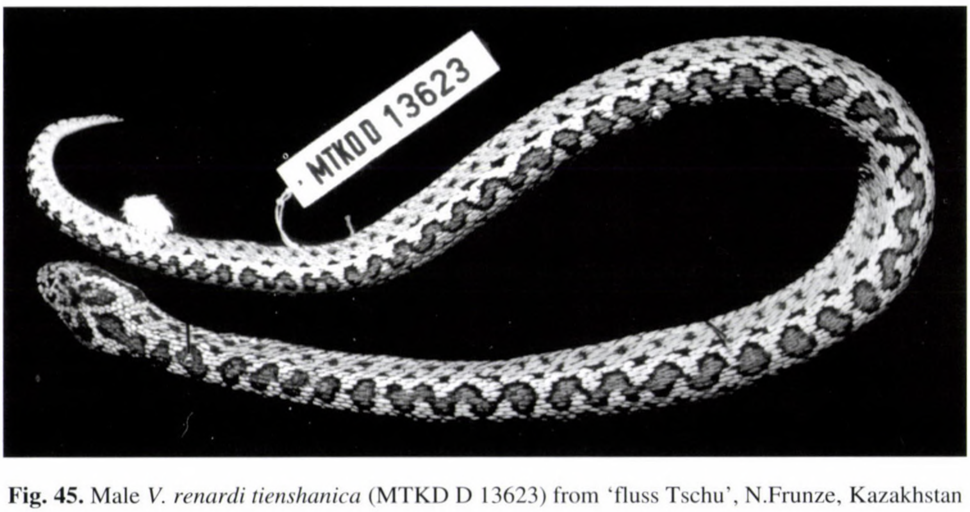


Fig. 45. Male *V. renardi tienshanica* (MTKD D 13623) from 'fluss Tschu', N.Frunze, Kazakhstan


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"Yugoslavian" localities, and material examined: Serbia & Montenegro: Durmitor, Skakala, 1520 m (MHNG 1355.42); Durmitor, Botun, 1850 m (MHNG 1355.41);

Bosnia & Herzegovina: Korita (ZIG 143–144, 241, GNM Re.ex. 4824–5, 4856–7, NMW 7012, 7015–20, ZIG 2 sloughs); Troglav, near Korita (MNG 7009); Bjelasnika Planina (GNM Re.ex. 1619); Mt. Lebrsmik, Cemerno (MHNG 1592.17–23); Baba Planina (NMW 7002, 7004–7007, 7008:1–3, 7010, 7011, 7013:1–3, 7014); Lebroznik (NMW 7029–30);

Croatia: Krk, Jezero (MZF 31887).

Vipera 'ursinii' graeca NILSON & ANDRÉN, 1988
"Greek meadow viper"
(Figs 19, 20)

Vipera ursinii graeca NILSON & ANDRÉN 1988, Zool. Scripta, 17: 311–314 (Figs 1–5) – Terra typica: Peristeri, Lakmos Mountains, Southern Pindos range, 1900 m altitude, Greece. Holotype: Göteborg Natural History Museum, Re.ex. 4942. Leg. NILSON & ANDRÉN 1986.

Description. It is a small-sized taxon. Maximum total length in our material is 40.2 cm for males (of which tail length is 5.4 cm), and 43.5 cm for females (tail 4.1 cm).

Head and body pattern much reduced. Belly-pattern whitish. No dark spots on cheek, labials and lateral and dorsal sides of head except narrow occipital and postorbital stripes; lateral sides of body light with blotches or spots absent (may be weakly visible in some males and juveniles); dorsal pattern consists of a band, which varies from being markedly tagged zigzag band with pointed corners of windings to a narrow straight vertebral stripe only.

Posterior supralabials markedly smaller than anterior ones in size (the three first supralabials very large while the following ones are much reduced: to less than half the height of the anterior ones; six to seven supralabials on each side and with the third under orbit. One to five loreals. Nasal mostly divided into two plates, normal, or united with nasorostralia; upper preocular often separated from the nasal; parietals divided.

An early reduction of dorsal scale rows (from 21 to 19 rows at the position between the third and the ninth ventral) i.e. 19 dorsal scale rows on neck and on anterior part of body, 17–19 at midbody; often around 15 anterior to anal plate. Low number of ventrals. Low number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 13–14 specimens of both sexes are as follows: preventrals: 1.54±0.14;

◄

Figs 56–57, 61, 63–65, 73–74. 56 = Live specimen of *Vipera eriwanensis* at lake Cildir, province Kars, East Turkey, while eating a *Lacerta valentinii*; 57 = Habitat of *V. eriwanensis* from terra typica at Ara Iler, N.Yerevan, Armenia. 61 = Habitat of *V. ebneri* at the Lar valley, Elburz Mountains, northern Iran. 63–65 = Live specimens of *Vipera* spp.: 63 = *V. lotievi* (ZIG), Chechenia, Russia, 64 = *V. darevskii* (ZIG), Mt. Legli, Armenia; 65 = *V. pontica*, holotype (GNM 5021), Coruh valley, prov. Artvin, Turkey. 73–74 = Habitat for *V. 'ursinii' rakosiensis:* Former habitat at lake Neusiedler, in Austria. All habitats for this taxon in Austria is at present changed into agricultural areas in a most efficient manner. The species is today extinct in Austria. Wine yard at lake Neusiedler. 74 = Dabas, south of Budapest, Hungary. Fire is another threat to this snake, as it kills both the snake, as well as some of its main prey items, *Lacerta agilis* and orthopterans. Unlawful, fields are set on fire rather regularly in order to quickly produce fresh grass for sheep and geese

ventrals: 123.92±0.51; scale rows on neck: 19.00±0.01; scale rows on midbody: 18.78±0.16; posterior scale rows: 15.14±0.23; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 5.77±0.46 and 4.62±0.39 respectively; supralabials (sum of both sides): 12.62±0.24; sublabials (sum of both sides): 16.23±0.43; circumoculars (sum of both sides): 16.77±0.53; loreals (sum of both sides): 4.15±0.44; crown scales (intercanthals and intersupraoculars): 10.85±0.64; dorsal windings/blotches: 54.10±1.20.

It is a taxon of the *Vipera ursinii* complex characterized by a unique serum albumin (JOGER *et al.* 1992, NILSON *et al.* 1993). By immunological results most similar to *macrops* together with which it forms an evolutionary lineage of common ancestry.

Diagnosis. Thus a taxon within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size

3. Non-bilineate body ground colour pattern

4. White belly

5. Lateral blotches and spots on body absent (but may be weakly visible in some males and juveniles)

6. No dark spots on labials and lateral and dorsal sides of head except narrow occipital and postorbital stripes

7. Dorsal zigzag band markedly tagged with pointed corners of windings, or consisting of a narrow vertebral line only.

8. Medium number of dorsal windings

9. Nasal normally divided into two plates or united with nasorostralia

10. Rostral as high as broad

11. A low loreal number

12. Few circumoculars

13. Upper preocular normally not separated from nasal

14. Fewer crown scales

15. More fragmented parietals

16. Lowest number of supralabials (6)

17. The three first supralabials very large, while the following ones are much reduced (less than half the height of the anterior ones)

18. Third supralabial below orbit

19. Few sublabials

20. Few mental scales

21. Early dorsal scale row reduction: 19 rows on anterior part of body and 17–19 at midbody

22. A low ventral number

23. No exposed intersquamose area

24. Lower number of subcaudals (lowest in the complex)

25. Being subalpine/alpine

External morphology evolved as typical for alpine taxa of the *ursinii* complex; similar to *ursinii* in various characters, but unique in combination of characters (posterior dorsal scale rows, supralabialia shape and numbers, fragmentation of frontal, shape of dorsal band). Similar to *macrops*, but differ in number of subcaudals, shape of nasal, lateral pattern, number of supralabials. Differs from lowland *V. u. rakosiensis* and *V. u. moldavica* by its smaller size, white belly, earlier dorsal scale row reduction, absence of black exposed intersquamose area, no bilineate ground colour, reduced postorbital band. It differs from lowland *renardi* and all Asian mountain taxa (except the Chinese *parursinii*) by having 19 midbody scale rows. Differs from all (except *anatolica*) by having a shorter tail with a lower number of subcaudals (lowest in the entire complex).

Of the examined 13 specimens, 92.3% had parietals divided, while 7.7% had not. Nasalia was undivided in 61.5% of the snakes, although always much semidivided. In 38.5% of the snakes the nasalia was divided into pre- and a postnasalia. In 46% of the specimens the nasalia was totally fused with the nasorostralia, and thus forming a large nasalia in broad contact with the rostral. Upper preocular in contact with nasalia on both sides in 61.5% of the snakes, on one side only in 15.4%, and with no contact in 23.1% of the snakes.

Habitat. This viper occurs in a subalpine environment at about 2000 m altitude (Fig. 21). Sympatric reptiles included *Lacerta agilis bosnica* and at somewhat lower altitudes, *Podarcis m. muralis, Lacerta t. trilineata* and *Coronella a. austriaca* and the amphibians *Bombina variegata scabra* and *Rana graeca*. Permanent snowfields occur frequently in the habitat, even at lower altitudes than where the meadow vipers occur. The habitat is typical for 'mountain *ursinii*' with rocky, stony subalpine meadows at around 2000 m altitude or slightly lower (NILSON & ANDRÉN 1988, NETTMANN *et al.* 1992)

Distribution (Fig. 69). The Greek alpine meadow viper is so far found in a number of alpine meadow habitats in the entire Pindos mountain range in Central Greece (DIMITROPOULOS 1985, pers. com. and in litt., CHONDROPOULOS 1989). These localities are the Tzoumerka mountain, Lakmos mountain (Peristeri), Koziakas mountain, Metsovon, Tsouka Karali, Tymphristos mountain and eventually in the mountains north of Ioannina. Today the Greek meadow viper is registered from around 12 places in Southern and central mainland Greece (DIMITROPOULOS pers. com., NETTMANN pers. com., IOANNIDES, pers. com.).

Estimated population size. Little is known about this taxon when it comes to density and conservation. The type locality might eventually be affected to some extent due to the construction of a huge water reservoir in that locality. According to DIMITROPOULOS (in litt.) the Greek meadow viper seems to be locally abundant. Our opinion from the type locality is the same. We found ten specimens during a

few hours in a small area of less than one hectare in the Lakmos mountain in July 1986. NETTERMAN (pers. com.) and three coworkers observed 12 specimens during one hour at a site in the Timfristos mountain range in May 1989. It is presently probably not highly endangered, although rather locally distributed.

Field observations. The habitat for *graeca* was grazed alpine meadow, with scattered junipers and stones. The density was comparatively high. The observed specimens were seen near smaller stones with some vegetation left unaffected by grazing. A high density of orthopterans was noted.

Taxonomic entity. *Vipera ursinii graeca* is a well-defined taxon, not close to any other here-examined sample. However, it has occasionally in literature been treated as a part of a larger assembly of taxa (as here defined) under the *name Vipera u. ursinii* (s. l.).

Greek localities and material examined. Greece: S. Pindos Mountains, Lakmos (GNM Re.ex. 4942 – Holotype; ZIG 145–147, 242 (+ 9 unregistered ZIG specimens) – Paratypes.

Vipera 'ursinii' rakosiensis MÉHELY, 1893
"Danubian meadow viper"
(Figs 22, 23)

Vipera berus rakosiensis MÉHELY, 1893, Zool. Anz. 16: 186–192. – Terra typica: Rákos, Budapest, Hungary, DELY (1983). Lectotype: British Museum (Natural History), No. 94.1.22. 21. Don. L. MÉHELY 1894.
Vipera ursinii, BOULENGER 1893a (part.), Proc. Zool. Soc., London 1893: 596–599 (pl. 51).
Vipera ursinii rakosiensis, KNOEPPFLER & SOCHUREK 1955. Burgenl. Heimatbl. 17(4): 185–188.

Comments. The type series consisted of four specimens, of which two were collected by O. HERMAN on the Rákos meadow in 1892 and placed in the Budapest University Collection (KORSÓS 1991). The other two were included in the University Collection already in 1872 as *Pelias berus*. The taxon was described by MÉHELY in 1893 (not 1894 as elsewhere stated – see DELY 1983). The type series stored in Budapest was destroyed during the political turbulence in 1956 (KRAMER 1961, KORSÓS in litt.). One specimen was donated by MÉHELY to the British Museum in 1894, and may have been a part of the type series. In any case, it is a lectotype (see above). Lectotype designation is by KRAMER (1961).

Description. It is a large-sized taxon. Maximum total length in our material is 48.0 cm for males (of which tail length is 5.3 cm), and 64.5 cm for females (tail 6.4 cm). However, another female with broken tail measured 66.0 cm full length.

Head and body pattern present. Belly-pattern black. Labial sutures without dark pattern. Have spots on cheek and lateral and dorsal sides of head, including broad occipital and postorbital stripes;

bilineate ground colour; lateral sides of body light with pronounced blotches or spots; dorsal pattern consists of a zigzag band with rounded corners of windings.

Normally eight supralabials on each side (occasionally from six to nine) and with the fourth under orbit. One to five loreals on each side. Nasal mostly normal with an upper nasal split; upper preocular normally in contact with the nasal; parietals normally undivided.

A later reduction of dorsal scale rows (from 21 to 19 rows at an average position near the 25th ventral) i.e. 21 dorsal scale rows on neck and on anterior part of body, 19 at midbody (meanwhile 21) and 17 anterior to anal plate. Medium number of ventrals. High number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values (±S.E.) for 60–64 specimens of both sexes are as follows: preventrals: 1.97±0.11; ventrals: 132.64±0.37; scale rows on neck: 20.47±0.13; scale rows on midbody: 19.23±0.08; posterior scale rows: 16.92±0.05; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 25.76±3.20 and 20.23±2.49 respectively; supralabials (sum of both sides): 15.67±0.12; sublabials (sum of both sides): 19.25±0.17; circumoculars (sum of both sides): 17.10±0.18; loreals (sum of both sides): 5.40±0.23; crown scales (intercanthals and intersupraoculars): 11.75±0.33; dorsal windings/blotches: 53.53±0.52.

It is a taxon of the *Vipera ursinii* complex characterized by a unique serum albumin (JOGER *et al.* 1992, NILSON *et al.* 1993). Based on immunological results perhaps most similar to mountainous *ursinii*.

Diagnosis. Thus a species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Large size
3. Bilineate body ground colour pattern
4. Black belly
5. Pronounced lateral blotches and spots on body
6. No dark spots on labial sutures, but dark band on lateral and dorsal sides of head, including broad occipital and postorbital stripes
7. Dorsal zigzag band with rounded corners of windings
8. Constant medium number of dorsal windings
9. Nasal normal with an upper nasal split
10. Rostral as high as broad
11. A low loreal number
12. Few circumoculars
13. Upper preocular often in contact with nasal
14. Medium to higher number of crown scales
15. Less fragmented parietals
16. Few supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Median number of sublabials
20. More mental scales
21. Delayed dorsal scale row reduction, 21 rows on neck and 19 on midbody

22. Median ventral number
23. Exposed black intersquamose area (one-third of scale width)
24. Higher number of subcaudals
25. Lowland meadow inhabitant

External morphology evolved as typical for lowland taxa of the *ursinii* complex; similar to *moldavica* in various characters but unique in combination of characters (labial pattern, frontal ocellated pattern, loreals, albumin profile). Different from *renardi* and the Asian alpine taxa (except *parursinii*) in number of midbody scale rows. Differs from alpine European (and *anatolica*) taxa by its bigger size, black belly, more posterior dorsal scale row reduction, presence of black exposed intersquamose area, bilineate ground colour, pronounced postorbital band.

The morphology is further described by KRAMER (1961), SAINT GIRONS (1978) and VANCEA *et al.* (1985).

Karyotype of *Vipera 'ursinii' rakosiensis* is normally 2N = 36 (16 V + 20 m) LIPTÓI *et al.* (1999)

Distribution (Fig. 69). Historically *rakosiensis* has had its distribution restricted to the Pannonian Basin. This late Tertiary basin is surrounded by the Carpathians, the Eastern Alps and the Dinaric Alps, and covers the whole of Hungary. It extends westwards as the Vienna basin into Austria, southwards into northeastern Serbia and eastwards into Transylvania in Romania (AGER 1980). The former distribution in Hungary has been discussed by several authors (e.g. DELY & JANISCH 1959, DELY 1978, TAKÁCS *et al.* 1987, KORSÓS 1991, STUMPEL *et al.* 1992, KORSÓS & FÜLÖP 1994). In addition, these authors (see conservation chapter) discuss the reasons for the decline.

CABELA and TIEDEMANN (1985) have discussed the former distribution in Austria. This European lowland meadow viper has in recent times been exterminated in many areas, and at present known only from two regions (four demes) in Hungary. It has recently become extinct in Austria and in Romania. The systematic position of the population that in the literature is thought to represent a case of secondary introgression with *renardi*, and that exists in Moldavia (VANCEA *et al.* 1985) will be discussed elsewhere in this paper. It is also said to occur in areas of northern (former) Yugoslavia at the Hungarian border (Slavonia) (MERTENS & WERMUTH 1960, BRELIH & DZUKIC 1974). The single record originates from a timber boat that was unloaded in Budapest, and which had arrived from Slavonia. The snake concerned was found on the bank in Budapest during unloading of the cargo (DELY 1986). Its possible Slavonian origin must be considered as unverified.

According to BESKOV (1973), the few specimens found at the beginning of this century in Bulgaria should be referred to this taxon (however see the discussion of *moldavica*).

The distribution in Hungary and Austria during the 19th century is to some extent discussed by e.g. MÉHELY (1894) and the situation during the first half of the 20th century by e.g. SCHWARZ (1936) and KRAMER (1961). The present situation is discussed here and by CORBETT (1989).

Estimated population size. In recent times, *rakosiensis* has been much exterminated, and it is presently known for sure only from two regions in Hungary. It has recently become extinct in Transylvanian Romania (KORSÓS & ÚJVÁRI 1998), and it is extremely rare in the four remaining Hungarian populations. However, in former days it had a high population density. The high density at Laxenburg in Lower Austria was in the last century pointed out by BOULENGER (1893*a*), but these populations have stayed healthy far into the 20th century (e.g. PSENNER 1939). In the surroundings of Laxenburg payments for killing of vipers resulted in more than 1,000 specimens of *rakosiensis* killed at this site in the year of 1892 (BOULENGER 1913). The Natural History Museum in Vienna has very large series of Austrian specimens in their scientific collection from this period. Today it seems to be totally extinct in Austria (GRILLITSCH *et al.* 1983, CORBETT 1986*a, b*, TIEDEMANN 1990, KAMMEL 1992*a, b*, and own obs.).

Habitat (Fig. 24). The Hungarian distribution and habitat choice is to a certain extent discussed by DELY (1978, 1987), DELY and JANISCH (1959), DELY and STOHL (1984). Description of habitats can be found in KRAMER (1961) and BRODMANN (1987), with good photographs in the latter. Various habitat alterations including road constructions are amongst the most severe threats in the Hanság area, Hungary (FÜLÖP 1992).

A summary of a botanical report of a typical habitat in June south of Budapest, made by ANTAL SÁNTA, botanist of the Ministry of Environment, and kindly supported by Dr. ZOLTÁN KORSÓS reads:

"The vegetation of the area is primarily influenced by the table of the soil water (its distance from the surface). The whole region is affected by the catastrophic water management of the last decades, which have accelerated the drying process.

The characteristic plant associations (in order from the wetter to the drier) are the followings:

1. Drying marshy meadow (*Succiso-Molinietum coeruleae*). Occupies the majority of the area. Characteristic plant species are: *Succisa pratensis, Schoenus nigricans*. In more moist places, remnants of separate association, *Schoenetum nigricantis*, can be found. There is also a fragment of a former *Calamagrosti-Salicetum cinereae* bog.

2. Sandy "puszta" meadow (*Astragalo-Festucetum rupicolae*) and sandy pasture (*Potentillo arenariae-Festucetum pseudovinae*). Occurs in somewhat higher

plateaus, a typical steppe vegetation. Characteristic species are: *Festuca rupicola, F. pseudovina, Stipa borysthenica.*

3. Calcaroeus sandy grassland (*Festucetum vaginatae danubiale*). Characterizes the highest places, usually on the top of former sand dunes. Very dry areas, the soil water table never reaches it. Characteristic species are *Stipa borysthenica, Festuca vaginata.*

These associations are not separated by clear edges but overlap each other according to the microgeography of the terrain. Hence, the area is unusually complex and rich in plant species. A slight degradation can also be observed due to the grazing activity and other human influences of the last decades. This can be followed by the presence of some weed species."

The pusztas of eastern Austria and northwestern Hungary (Hanság) contain over 50% of its recent historical distribution but now have less than 5% of its populations. The pusztas of Central Hungary now have 95% of what is left (CORBETT 1992, 1993).

Field observations. This taxon was observed a number of times during fieldwork for the SEH Conservation Committee (see the Material and Methods section). We visited both the known Austrian sites and the Hungarian ones. In Austria, no trace of any remaining population could be found. The remaining parts of the habitat seem far too small and are still diminishing as time goes by. Grape and sunflower plantations nowadays cover almost all of the old sites. At Moosbrun a local worker told us in 1989 (SEH: CC) about an observation of a big "Kreuzotter" that he observed a few years back, and this might well have been a *rakosiensis*. No additional observations have been made recently (KAMMEL 1992*a, b*).

Small patches of possibly suitable habitats were observed in the former military zone ("Iron curtain") between Austria and Hungary from the Austrian side along the border. On the Hungarian side, at Hanság, there still exists a population, and at two of our three visits, we observed specimens at this locality. The habitat is protected and consists of fenced virgin "Puszta" meadow that is cut once or twice a year. Here we observed in sympatry *Coronella a. austriaca, Anguis f. fragilis* and *Natrix n. natrix*. In wetter areas nearby we also found *Pelobates f. fuscus, Rana arvalis wolterstorfii, Rana dalmatina, Bombina bombina.*

The remaining and still best populations of *rakosiensis* occur in the "puszta" meadows in the flat lands between the rivers Danube and Tisza south of Budapest (Fig. 24). Here we have made about 20 observations during our work at three different localities. Our observations include a pregnant female with aberrant pattern (see Fig. 23, and in CORBETT 1989). This female later gave birth to nineteen young (JANISCH 1993) of which 13 were aberrant in the same way (Fig. 23). All these youngs were released together in the same season with the female at the site of ori-

gin (KORSÓS, pers. com.). In the same area both juvenile specimens and adults of different size, including some pregnant females were observed. In our opinion this is a good population that can survive for a longer period if the areas of good habitat are allowed to remain.

Since the 7th of April, 1993, a key part of the habitat was declared as a 'Landscape Protection territory' (order No. 17/1993 (IV.7.) KTM) by the Hungarian Ministry of Environment and National Authority for Nature Conservation, and the areas are protected by the Hungarian Nature Conservation Legislation of 1974 (KORSÓS 1991). The SEH, through its Conservation Committee, has succeeded to buy further private land in order to turn it into a permanent Nature Protected Area in cooperation with the Hungarian Society for Ornithology and Nature Conservation. Again, the habitat consists of grazed meadows with a mosaic of drier and more wet areas. In sympatry we found *Coronella a. austriaca*, and also *Natrix n. natrix, Lacerta a. agilis, Lacerta v. viridis, Podarcis taurica, Bufo v. viridis* and *Rana ridibunda*.

Taxonomic entity. *Vipera ursinii rakosiensis* is a well-defined taxon, not close to any other here-examined sample. However, occasionally some or all of the Romanian/Bulgarian populations, here defined as *Vipera u. moldavica*, have been included.

Austrian and Hungarian localities, and material examined. Austria: Laxenburg (GNM Re.ex. 1464, 1920, ZMK 68131); "Wien" (GNM Re.ex. 1986); "Basse Autrich" (NMHG 1120.86); Niederösterreich, Grammat-Neusiedl (NHMG 1354.21?–23, 1354.26–30); "zwischen Mariental und Ebergassing (NMHN 1978.438).

Hungary: "Budapest" (ZIG 156–157, 250); Komitat Pest (NHMG 1354.47–50, 1354.53–54, 1354.59); 1 slough "Budapest"; Ócsa (HNHM 1 specimen); Felsőbabád (Ócsa)(HNHM 3 specimens); Dabas (HNHM 1 specimen, NHMG 1354.11–20, 1354.25, 1354.33–6, 1354.40–1 1354.43–5); Soroksár (HNHM 2 specimens); Kunpeszér (NHMG 1354.37–8, 1354.42, 1354.56–8); Bugac-Puszta (HNHM 1 specimen).

Vipera 'ursinii' moldavica NILSON, ANDRÉN et JOGER, 1993 "Moldavian meadow viper" (Figs 25, 26)

Vipera ursinii moldavica NILSON, ANDRÉN et JOGER, 1993. Amphibia-Reptilia 14: 45–57. – Terra typica: Valea lui David, Jasi, Romania. Holotype: GNM Re.ex. 5057, Leg. DZIUBINSKI 1988.

Description. It is a large-sized taxon within the *ursinii* complex. Maximum total length in our material is 55.6 cm for males (of which tail length is 6.9 cm), and 53.0 cm for females (tail 5.0 cm).

Head and body pattern present. Belly-pattern black. Labial sutures with dark pattern; broad occipital and postorbital stripes on lateral and dorsal sides of head; bilineate ground colour; lateral

sides of body light with pronounced blotches or spots; dorsal pattern consists of a zigzag band with rounded corners of windings.

Eight to nine supralabials on each side (occasionally from seven to ten) and with the fourth under orbit. Two to eight loreals on each side. Nasal mostly normal with an upper nasal split (75%); upper preocular in contact with the nasal in half of the cases; parietals divided in half of the cases.

A later reduction of dorsal scale rows (from 21 to 19 rows at an average position near the 27th ventral) i.e. 21 dorsal scale rows on neck and on anterior part of body, normally 19 at midbody (meanwhile 21) and 17 anterior to anal plate. High number of ventrals. High number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 43- 44 specimens of both sexes are as follows: preventrals: 1.82±0.13; Ventrals: 138.98±0.48; scale rows on neck: 20.19±0.16; scale rows on midbody: 19.34±0.15; posterior scale rows: 16.56±0.14; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 26.42±5.03 and 18.77±3.55 respectively; supralabials (sum of both sides): 16.98±0.17; sublabials (sum of both sides): 19.41±0.21; circumoculars (sum of both sides): 18.45±0.27; loreals (sum of both sides): 8.70±0.35; crown scales (intercanthals and intersupraoculars): 11.91±0.45; dorsal windings/blotches: 57.28±0.85.

A taxon of the *Vipera ursinii* complex characterised by a unique serum albumin (Fig. 67, and NILSON *et al.* 1993). Genetically close in serum albumin and immunological distance to the Balkan Peninsula *graeca* and *macrops*.

Diagnosis. A taxon within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Large size
3. Bilineate body ground colour pattern
4. Black belly
5. Pronounced lateral blotches and spots on body
6. Dark sutures on labials (in more than 80% of the cases), and dark bands on lateral and dorsal sides of head, including broad occipital and postorbital stripes
7. Dorsal zigzag band with rounded corners of windings
8. Constant medium number of dorsal windings
9. Nasal with an upper nasal split in half of the cases
10. Rostral as high as broad
11. A high loreal number
12. More circumoculars
13. Upper preocular in contact with nasal in half of the cases
14. Medium to more crown scales
15. Parietals fragmented in half of the cases
16. Few to more supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. More sublabials
20. More mental scales

21. Delayed dorsal scale row reduction, 21 rows on neck and 19 on midbody (normally)

22. Higher ventral number

23. Exposed black intersquamose area (one-third of scale width)

24. Higher number of subcaudals

25. Lowland meadow inhabitant

External morphology evolved as typical for lowland taxa of the *ursinii* complex; similar to *rakosiensis* and *renardi* in various characters but differs from both in combination of characters (labial pattern, frontal ocellated pattern, loreals, albumine profile). It differs from *renardi* by normally having 19 midbody scale rows (21 in *renardi*); a lower number of ventrals and supralabials. Compared to *rakosiensis* it has a higher number of ventrals and supralabials. Different from the Asian alpine taxa (except *parursinii*) in number of midbody scale rows. Differs from alpine European taxa (and *anatolica*) by its larger size, black belly, more posterior dorsal scale row reduction, presence of black exposed intersquamose area, bilineate ground colour, pronounced postorbital band. A pronounced ocellated dark and light-edged frontal spot separates it from all other taxa in the *ursinii* complex. Specimens with frontal spots are frequent in populations of other taxa, but the frontal spot is never pronouncedly ocellated.

VANCEA and IONESCU (1954) and FUHN and VANCEA (1961) give additional information of the morphology of the population at Jasi (Valea lui David). The morphology is further described by VANCEA *et al.* (1985).

Comments. At least one single population has until recently occurred on hilly meadows in the Carpathian Mountains of Romania. In 1957, Prof. VANCEA together with a student collected two specimens at a meadow at 950 m altitude south of Mt Rarau. Both specimens were deposited at the Natural History Museum in Jasi, but are now lost (VANCEA, pers. com.). We have examined a series of photos of one specimen, a single subadult female from this locality, and some additional information of the pholidosis of this specimen has been published by VANCEA *et al.* (1985). This specimen is characterised by being 290 + 33 mm long, and by having the frontal undivided and parietals divided, 12 intercanthals and intersupraoculars, nine and 7 circumoculars, 19 midbody scale rows, 130 ventrals and 27 subcaudals. Colour on ventral side of body said to be light (VANCEA *et al.* 1985) and by KRECSÁK and ZAMFIRESCU (2001).

The main distribution for *moldavica* is in Romania, and discussed by FUHN and VANCEA (1961) and VANCEA *et al.* (1985) under the name *rakosiensis*/*renardi* in Moldavia and as *renardi* in the Danube Delta area. However, the distribution possibly also includes Bulgaria. The old samples at Sofia and Sumen (BURESCH & ZONKOW 1932) are thoroughly discussed by BESKOV (1973) and are regarded by

him as *rakosiensis*. The sites are situated geographically between Moldavia and the *macrops* region in former Yugoslavia, and can be considered as a part of this phylogenetic lineage. We have had access to a larger series of photographs of all Sofia Museum specimens (Figs 27, 28) from Bulgaria, and the specimens can equally well be referred to *moldavica* as to *rakosiensis*. The Bulgarian populations now seem to be extinct due to habitat alterations, and a definite conclusion might be problematic without material for genetic analyses.

According to the photos examined of the female from Mt. Rarau, it is most similar to the female from Sofia, Bulgaria, which was collected at similar altitude (950 m) (BESHKOV 1973). The Sofia specimen was found in a similar kind of hilly habitat (TAKÁCS, pers. com.). Both have a broad band running from the corner of mouth to the posterior border of the eye. This band covers most of the last third maxillary plate. The Mt. Rarau female seems to be of similar '*rakosiensis* type' of *moldavica*, as the Bulgarian ones and we do not hesitate to include it into this taxon. Both specimens also share the (plesiomorphic) occipital spot with the other east Romanian specimens and with *renardi*. The Mt. Rarau population is perhaps extinct today. The meadows south of Mt. Rarau have been heavily grazed and cultivated, forests have been cut and replanted. The same has happened to the habitat at the Sofia locality in Bulgaria. These populations are probably swept out due to habitat alterations. We were unable to find suitable habitats left at Mt. Rarau during a visit in July 1988.

As shown from 'The fossil record' (see below), lowland '*ursinii*' s. l. represents series of ancestral faunistic components of the mid-European steppe ecosystems. The occurrence of *moldavica* (or *rakosiensis*) in the mountains around Sofia at 900 m altitude and at Mt. Rarau, also 900 m altitude, suggest that the species could disperse across mountains of that altitude.

The Moldavian population has been looked upon as an intergrading population between *rakosiensis* and *renardi*. This has been the traditional view (e.g. VANCEA *et al.* 1985) based on mean values of several morphological characteristics between these two taxa. VANCEA *et al.* (op. cit.) state that this taxon is similar to *rakosiensis* in about 75% and to *renardi* in 25% of the pholidosis. The Danube Delta population is similar, but with the percentage of similarity reversed (i.e. 75% as *renardi*; 25% as *rakosiensis*). We have found a somewhat similar pattern, although with less pronounced differences (NILSON *et al.* 1993, and Table 47).

The phylogenetic analyses based on immunology gave the results that the *renardi* and *rakosiensis* branches have a joint common ancestor, and that *moldavica* (through the Jasi population) is a sister group to that lineage (JOGER *et al.* 1992). The phylogenetic analyses based on morphometrics gave the results that *moldavica* and *rakosiensis* have a joint common ancestor, and that the *renardi*

group of taxa is the sister clade to that lineage. In both sets of analyses, *moldavica* is a sister taxon to *rakosiensis* and all other European Mountain taxa. The Danube Delta population is probably a recent sister group to the Jasi population and here we include it in *moldavica*. Close genetic relationship between these two populations has been stressed by KOTENKO *et al.* (1999).

The complex picture of the morphology seen in the Jasi and Danube population could hypothetically also be a result of true sympatry between *renardi* and *'rakosiensis'* (the holotype of *moldavica* is of the *'rakosiensis'* morph). The blood used in the immunological investigation and for the electrophoretic profile came from a specimen of the same kind (see NILSON *et al.* 1993: Fig. 5)). A re-analysis of the pholidosis of the Romanian populations (based on own measurements) shows that the individuals at Jasi may not be intermediates between *renardi* and *'rakosiensis'* (=*moldavica)* (see above). They could possibly be a mixed population of the two, where 75% are *moldavica* at Jasi and 25% in the Danube Delta population, with remaining ones being *renardi*. If so this would verify the species status of these two taxa in sympatry, in spite of the occurrence of single hybrids (Figs 29, 30). In such a case, some ecological factor would separate them in nature (microhabitat choice, moisture gradient etc.), that perhaps no longer can be fulfilled at Jasi due to habitat destruction.

We only observed the *'rakosiensis'* type of *moldavica* in the field during our stay at Jasi in 1988. Further, an examination of a series of four juveniles from the Danube population (MNHG 1354.66–68) showed one specimen with relative late level of scalerow reduction and three specimens with early. These specimens may have originated from the same brood (no information about this in the Museum file) and both types of morphs in the same (presumed) clutch do not support a hypothesis of the two species in sympatry. No clutch from the Moldavian group has been available for examination (comp. Fig. 7).

The level of dorsal scale row reduction shows a strange, but similar pattern in the Moldavian and the Danube populations. The level of reduction is either anterior on body (19 midbody scale rows) or posterior (21 midbody scale rows). The first is dominating in the '*rakosiensis* morph' of *moldavica* and the latter in the '*renardi* morph', and thereby mirroring the actual situation in "true" *rakosiensis* and *renardi*. There is no correlation between body size and level of reduction in these taxa, but in *moldavica*, a special pattern can be seen. The majority of specimens have an anterior reduction while the rest have a posterior one, and in the latter group increased bodysize seems to be positively correlated with a more posterior level of scale reduction (Fig. 7). The same pattern persists if the two samples are analysed separately, although less strong in the Danube Delta sample due to the low number of specimens. In addition, when the Moldavian sample is divided

Table 47. Variation, given as mean (X), range, and coefficient of variation (C.V.) of selected morphological characters in the populations of supposed secondary introgression (=*moldavica*). Compared samples are: *V. u. moldavica* Jasi/Romanesti areas, *V. u. moldavica* Danube Delta, "*V. renardi*" morph (Fig. 29) of Jasi/Romanesti populations, "*V. u. rakosiensis*" morph (Fig. 30) of Jasi/Romanesti populations, true *V. renardi* (ile Orlov, Ukraine), true *V. u. rakosiensis* (Dabas, Hungary)

	N	Dorsal scale rows								
		Neck			Midbody			Posterior		
		X	range	c.v.	X	range	c.v.	X	range	c.v.
V. renardi (Orlov)	8	21	21–23	3.3	21	21		17	17	
Danube total	9	21	21		20	19–21	5.3	17	15–19	6.2
Jasi/Rom. total	32	20	17–21	5.6	19	17–21	4.9	16	15–17	5.3
Jasi '*ren.*-morph'	6	21	21		21	20–21	2.0	17	17	
Jasi '*rak.*-morph'	25	20	17–21	5.7	19	17–19	2.9	16	15–17	5.5
V. u. rakosiensis (Dabas)	22	21	19–21	4.2	19	19–21	2.2	17	16–17	1.3
	N	Dorsal scale row reduction*			Supralabials**			Sublabials**		
		X	range	c.v.	X	range	c.v.	X	range	c.v.
V. renardi (Orlov)	8	97	89–105	6.6	18	18		20	20–21	1.8
Danube total	9	43	12–90	81.1	18	16–19	5.8	20	18–23	8.4
Jasi/Rom. total	32	23	2–106	141.9	17	15–20	6.8	19	16–21	6.1
Jasi '*ren.*-morph'	6	87	64–103	17.4	18	16–18	4.8	19	16–21	9.6
Jasi '*rak.*-morph'	25	8	2–24	63.1	17	15–20	6.9	19	17–21	5.3
V. u. rakosiensis (Dabas)	22	23	6–100	93.1	16	13–17	5.8	20	18–22	7.2

* Position of dorsal scale row reduction given as corresponding ventral plate number

** Supra- and sublabials counted as sum of right and left sides

down to its two original localities, Valea lui David, and Romanesti, this pattern persists. This positive correlation in the *'renardi'* type of *moldavica* is obvious also when the whole sample is involved. However, this pattern can not be seen in true *renardi* or in *rakosiensis*, which otherwise are variable taxa in this aspect (Fig. 6). Neither can it be seen in any other investigated sample.

Although not demonstrated it could be interpreted that the level of dorsal scale row reduction moves (!) backwards along the body with growth in *moldavica*, a phenomenon never reported earlier in snakes. However, to demonstrate this, juvenile specimens of *moldavica* of the *'renardi'* morph have to be raised in captivity, or better, regularly recollected and measured in a study population in the field.

Distribution (Fig. 71). The main distribution for *moldavica* is in Romanian Moldavia and in the Danube Delta region. In Romania the range also includes the Carpathian Mountains at 950 m altitude south of Mt. Rarau, although the present situation for this population in unclear. The Moldavian localities in Romania are Valea lui David, Jasi; Calarasi-Dorohoj, Jud. Botosani and Romanesti, Ursaia, Jud. Jasi.

The Danube Delta localities are C. A. Rosetti, Danube Delta; Dobrudja Danube Delta, Grindul Saraturi Bratul Sf. Gheorghe and Grindul Perisor. Further additional literature refers to Caraorman (EDBERG 1984), Letea forest and Periteasca (TÖRÖK 1996).

From the Republic of Moldavia (Bessarabia) a single specimen is deposited in the collection in Natural History Museum in Kiev (SHCHERBAK, pers. comm.). Today it seems to be totally extinct, as all potential habitats are detoriated by agriculture, and no legal or practical recovery programme exist (KORSÓS & ÚJVÁRI 1999)

As discussed above we also include Bulgaria with the Sofia and Sumen samples into the range of this taxon (Liulin Mountains, W Sofia, Monastery Sveti Kral; Sumen, Koskovete (Kolavavgrad)).

Estimated population size. Nothing is known about the present situation, but most certainly very rare in the Moldavian plains. The situation is better in the Danube Delta area, where a new Biosphere Reserve has been established (CORBETT in litt., TÖRÖK 1996). Since the beginning of this century, it has not been found again in Bulgaria, where it probably become extinct due to habitat destruction (TAKÁCS, in litt.).

Habitat and field observations. Very small fragments of the original habitat remains. The Moldavian plains are a landscape characterised by undulating hills with more dry and moisture areas intermixed. We have visited one of the very few remaining habitats (perhaps the only one left), Valea lui David, outside Jasi (Fig. 31). This locality is situated in the middle of a series of enormous monocultures that cover the major part of the Moldavian plain. Together with Prof. VANCEA we observed two semiadult specimens and in sympatry *Coronella a. austriaca* and *Lacerta agilis chersonensis*. The area with a partly heavily grazed meadow on gentle sloping hillside is comparative small, about 50 hectares. Description of habitats can be found in BRODMANN (1987), with a good habitat photograph from Jasi under the section of Moldavian and Danube delta populations of *'renardi'*. The soil is sandy and *Stipa pennata* is a characteristic grass species in the meadow.

A closer study has been performed in the Danube Delta by ZSOLT TÖRÖK, Danube Delta Institute, Tulcea, Romania. According to this source (through the courtesy of ZOLTÁN KORSÓS, Budapest) the soil in the habitat is predominantly

marine sandy soils, with less than 5% clay (Fig. 32). The snake habitat is in a *Juncus* zone between sanddunes and reed belts. The structure vary between localities. At Periteasca there is a mosaic of halophilous vegetation (*Typha angustifolia* and *Bolboschoenus maritimus*) and less saline patches with *Puccinella convoluta, Limonium gmelini* and *Juncus maritimus*. At Sfintu Gheorghe forestry polder (*Fraxinus*) and at Letea xerophilous dune grassland with *Carex colchica, Ephedra distachia, Secala sylvestre* and *Festuca beckeri* dominating, and with *Quercus pedunculiflora* and *Fraxinus pallisiae* between the dunes. In the habitat the snake is sympatric with *Lacerta agilis chersonensis (=L. a. euxinica)*, and occasionally with *Natrix natrix* and *Hyla arborea*. In the reed belt *Triturus vulgaris, T. cristatus, Rana ridibunda* and *Emys orbicularis* also occur. The outer pure sand dune zone (with *Salicornia herbacea* and *Juncus* sp.) is inhabited by *Pelobates syriacus, P. fuscus* and *Eremias arguta*.

Further descriptions of the habitats can be found in FUHN and VANCEA (1961) and VANCEA *et al.* (1980, 1985).

Taxonomic entity. *Vipera ursinii moldavica* is a well-defined taxon, not close to any other sample examined here. However, it was originally considered as a part of *Vipera u. rakosiensis*, or treated as a hybrid population between *rakosiensis* and *renardi*.

It has been argued in the literature that the Moldavian mainland populations and the Danube Delta series could be treated as two separat taxonomic entities, which to some extent can be justified on morphological basis. However, due to overlapping pholidosis between the two series of populations, and to supposed genetic similarities we treat the two series as a single taxon. Additional reseach might modify this conclusion.

Romanian and Bulgarian localities and material examined. Romania: Valea lui David, Jasi, Moldavia. One specimen (GNM Re.ex. 5057 – Holotype); 10 unregistered specimens (MINJ, Paratypes); four specimens (NHMG 1354.31–2, 1354.39, 1354.46 – Paratypes); one specimen (ZIG 0283); Calarasi-Dorohoj, Jud. Botosani. One unregistered specimen (MINJ); Romanesti, Ursaia, Jud. Jasi. 17 unregistered specimens (MINJ); C.A.Rosetti, Danube Delta. Two unregistered specimens (MINJ); Dobrudja Danube Delta, Grindul Saraturi, Bratul Sf. Gheorghe. Three specimens (MNHG 1354.62–64); Danube Delta. Four specimens (NHMG 1354.65–68); Danube Delta, Grindul Perisor. One specimen (MTKDD 25506); Mt. Rarau, 870 m. One specimen (MINJ, now lost (inf. and photo from Prof. VANCEA + literature)).

Bulgaria: Liulin Mountains, W. Sofia, Monastery Sveti Kral (ZIS specimens a-b); Sumen, Koskovete (Kolavavgrad) specimens c-d).

Vipera renardi renardi (CHRISTOPH, 1861) "Lowland steppe viper" (Figs 33–36, 38–39)

Coluber foetidus GÜLDENSTEDT, 1801 (nomen oblitum) in Georgi, Geogr.-phys. naturhist. Beschr. Russ. Reich., 3 (7): 1884. – Terra typica: "Tawrow at Don and Tambow in the Steppe"

Pelias renardi CHRISTOPH, 1861 (nomen conservandum), Bull. Soc. Imp. Nat. Moscou 34: 599–606. – Terra typica: Sarepta, lower Volga, Russia. Type: lost. Topotype in British Museum (BMNH 1893.11.18.1), depicted in BOULENGER 1893*b*: plate LXIV).

Vipera berus, part., STRAUCH 1869, Syn. Viper. p. 32; 1873, Schl. Russ. R. 206.

Vipera renardi BOULENGER 1893*b*, Proc. Zool. Soc., London, 1893: 596–599 (pl. 64).

Acridophaga uralensis T. REUSS 1929, Wochenschr. Aquar. Terrar. K. Braunschweig 26. – Terra typica: Ural Mountains, Russia

Vipera ursinii renardi SCHWARZ 1936, Behringwerk-Mitt., Marburg, 7.

Vipera berus var. *renardi* BASOGLU 1947, Re. Facult. Sci. Univ. Istanbul 12B: 182–190.

Vipera ursinii renardi, (part). KRAMER 1961. Rev. Suisse Zool. 69: 627–722 (his "nordwestliche Steppenform").

Description. It is a large sized taxon within this complex. Maximum total length in our material is 60.7 cm for males (of which tail length is 6.8 cm), and 60.0 cm for females (tail 5.5 cm).

Head and body pattern present. Belly-pattern black. Labial sutures often with dark broad pattern; broad occipital and postorbital stripes on lateral and dorsal sides of head; weakly developed bilineate ground colour; lateral sides of body light with pronounced blotches or spots; dorsal pattern consists of a zigzag band with rounded corners of windings, or divided into rounded spots.

Normally nine supralabials on each side (occasionally from seven to ten) and with the fourth under orbit. Two to six loreals on each side. Nasal mostly normal, occasionally with an upper nasal split (in less than 40% of the cases); upper preocular in contact with the nasal in most of the cases; parietals occasionally divided (in less than 40% of the cases).

A markedly late reduction of dorsal scale rows (from 21 to 19 rows at an average position near the 96th ventral) i.e. 21 dorsal scale rows on neck, anterior part and midbody, and 17 anterior to anal plate. High number of ventrals. High number of subcaudals.

In tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 66–68 specimens of both sexes are as follows: preventrals: 2.20±0.08 (2.29±0.14 for the west *renardi* populations, 2.11±0.11 for the east *renardi*); ventrals: 142.93±0.46 (141.52±0.58 and range135–148 for the west *renardi* populations, 144.20±0.65 and range 135–151 for the east *renardi* populations); scale rows on neck: 21.22±0.07 (21.35 ±0.13 for the west *renardi* populations, 21.14 ±0.08 for the east *renardi*); scale rows on midbody: 20.94±0.05; posterior scale rows: 17.05±0.03 (17.00 ±0.05 for the west *renardi* populations, 17.09 ±0.05 for the east *renardi*); level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 95.28±1.31 and 66.82±0.88 respectively (96.41±1.64 for the west *renardi* populations, 94.03±2.18 for the east *renardi* (in%)); supralabials (sum of both sides): 17.94±0.08 (17.79±0.15 for the west *renardi* populations, 18.06±0.08 for the east *renardi*); sublabials (sum of both sides): 20.03±0.15 (20.28±0.23 for the west *renardi* populations, 19.84±0.22 for the east *renardi*); circumoculars (sum of both sides): 18.77±0.19 (18.07±0.26 for the west *renardi* populations, 19.38±0.25 for the east *renardi*); loreals (sum of both sides): 8.66±0.24 (8.71 ±0.36 for the west *renardi* populations, 8.61±0.35 for the east *renardi*); crown scales (intercanthals and intersupraoculars): 11.15±0.34 (9.97±0.43 for the west

renardi populations, 11.94±0.48 for the east *renardi*); dorsal windings/blotches: 59.41±0.62 (58.07±0.80 for the west *renardi* populations, 60.43±0.93 for the east *renardi*).

A taxon of the *Vipera ursinii* complex characterised by a unique serum albumin. In serum albumin pattern and the immunological reaction, it is most similar to the subalpine Armenian taxon *eriwanensis*. Serum profile somewhat different when comparing east and west *renardi* (Fig. 67, and JOGER *et al.* 1992, NILSON *et al.* 1993). In addition, in scalation characters a certain east-west difference can be seen.

(Here and in all tables, *renardi* includes all lowland samples from the range covering Russia, Ukraine and Kazakhstan, including a few specimens without more exact locality than Russia. In the *renadi* (west) (no. 13), and *renardi* (east) (no. 14) only specimens with exact localities are included. The 'Altai form of renardi' (no. 15) and the Chinese populations are not included in any of these three categories of *renardi*.)

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Large size
3. Weakly bilineate body ground colour pattern
4. Black belly
5. Pronounced lateral blotches and spots on body
6. Normally pronounced dark sutures on labials, and on lateral and dorsal sides of head, including broad occipital and postorbital stripes
7. Dorsal zigzag band with rounded corners of windings
8. Very variable number of dorsal windings
9. Nasal with an upper nasal split in less than half of the cases
10. Rostral as high as broad
11. A high loreal number
12. More circumoculars
13. Upper preocular in contact with nasal in most of the cases
14. Less crown scales
15. Parietals fragmented in less than half of the cases
16. Many supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Many sublabials
20. More mental scales
21. Posterior dorsal scale row reduction, 21 rows on neck and on midbody
22. High ventral number
23. Non-exposed intersquamose area
24. Higher number of subcaudals
25. Lowland steppe inhabitant

When tested with Fisher's Post Hoc test (PLSD), the west and east subsamples of *renardi* differ significantly in the number of circumoculars (p=0.001),

where the west sample has a mean value of 18.07±0.26 S.E, and the east sample has 19.4±0.25 S.E. With this test, they also differ in the number of ventrals (p=0.0002), where the west sample has a mean value of 141.5±0.58 S.E. and the east a mean value of 144.2±0.65 S.E.

External morphology evolved as typical for lowland taxa of the *ursinii* complex. Some similarity with *rakosiensis* and *moldavica* in various morphological characters, but both in combination of characters (midbody scale rows and dorsal scale row reduction level, labial pattern, ventral number, upper nasal split, snout shape). From the (hypothetical) parapatric *moldavica* it shows high genetic divergence (D=0.17, Nei Genetic Distance, KOTENKO *et al.* 1999). Differs from alpine European taxa, as well as Asian *anatolica* and *parursini* in number of midbody scale rows, in larger size, black belly, more posterior dorsal scale row reduction and pronounced postorbital band. Karyotype of a female *Vipera renardi* from the northwestern part of the range (Sterletskaya steppe, Kursk province, Russia) is 2n=36, NF=50 (PUZACHENKO *et al.* 1997). In addition, these authors indicate a difference in W-chromosome morphology between *renardi* and *rakosiensis*.

Some literature reports of *renardi* with nineteen dorsal scalerows (e.g. BOULENGER 1893*b*, DELY & STOHL 1989*a*) can be traced back to the Central Asian mountain form (*tienshanica*).

Morphological differences between *renardi* and southern 'subspecies' (=*ebneri* and *eriwanensis*) in Azerbaijan are to some extent discussed by ALIEV and GANIEV (1985).

In the morphological analysis and description of *renardi*, SAINT GIRONS (1978) follows KRAMER (1961) by also referring *Vipera dinniki* to this taxon. KRAMER, in his study, also included one specimen of the Armenian population later described as *Vipera darevskii*.

Distribution (Figs 71, 72). The distribution of *renardi* in former USSR is given by several authors (e.g. NIKOLSKY 1964, TERENTEV & CHERNOV 1965, BANNIKOV *et al.* 1977). The lowland steppe viper, as here defined, has had a large, but scattered distribution in the steppe zones of East Europe and West Asia. It is synonymous with the "western *renardi*" (sensu MÉHELY 1911) as well as "nordwestliche Steppenform" (sensu KRAMER 1961) found on the steppes of Southwestern and Central Russia, Kazakhstan and Ukraine, including Crimea. It has been stated to be abundant. This is, however, no longer the case in the European parts of its range (NIKOLAI ORLOV, in litt). Due to intensive grazing and agriculture in most of the original steppes, an extensive fragmentation of the habitats has taken place, with a dramatic decline in total population size. Today, only fragments of a once larger distribution persist, and often in very small pockets with low population densities (SHCHERBAK, TOKAR, ORLOV, TUNIYEV, pers. comm.). The main

occurrence is fragmented into small patches along river valleys in the old steppe habitats. The distribution is also to some extent discussed by VEDMEDERJA (1981) and KOTENKO (1981).

Its western border might be found close to eastern Romania (the Danube Delta populations are here included in *moldavica*). The species is found up to Pereyaslav (Perejaslas-Chmelnickij) southeast of Kiev, Ukraine (SHCHERBAK, pers. comm.), and this is the northernmost present population in Europe. Its (*renardi* s. l.) easternmost occurrence is near China, but the populations at northern Xinxiang, China, mentioned by BANNIKOV *et al.* (1977) and ZHAO and JIANG (1979) are here included in *tienshanica*. In addition, the steppe viper is stated to occur in the border areas of Mongolia on the Western Chinese slopes of the Altai Mountains (OBST 1963, BORKIN *et al.* 1990), but has up to now not been encountered in Mongolia proper. However, these Altai populations are here considered to belong to the 'Altai form of *renardi*' (see below), and we could not verify the presence of *renardi* (s. str.), as here defined, in China.

The occurrence of *renardi* in Azerbaijan is mentioned by ALEKPEROV (1978). It seems to penetrate from the north along the Caspian Sea shores into that republic. This concerned the lowland areas to the northeast, and we agree after examining preserved and live specimens from northern Azerbaijan. The species seems to have penetrated southward around the eastern side of the Great Caucasus to these plains. Through the courtesy of Boris Tuniyev we have received a live specimen of what seems to be typical *renardi* from the vicinity of the town Shemakha (Shemacha), Azerbaijan, found in a steppe habitat at 700 m altitude (ALEKPEROV 1982). ALEKPEROV (1978) gives mountain steppe at 600 m altitude as habitat in this region.

Estimated population size. It is now considered to be very rare in Ukraine (KOTENKO 1989) and in Kazakhstan due to habitat alterations. However, undisturbed populations still occur, sometimes with a high populations density. On the Urkrainian island of Orlov, in the Black Sea, the density can still be between 10 and 25 specimens per hectare (KOTENKO 1989), and with some specimens reaching 70 cm in length.

The occurrence seems to be restricted to untouched steppe habitats, and in Ukraine, the vast majority of these types of habitats have been turned into agriculture. In Kazakhstan, larger areas of original steppe habitats have been altered into secondary dry land with a collapsed original steppe fauna and flora with low diversity. Therefore, *renardi* is today absent from large regions of Kazakhstan that were originally populated. However, still there seem to be local abundant populations in sections of large steppe habitats that remain (Fig. 37). PARASKIV (1956) gives the distribution for Kazakhstan. DJUSEBAJEVA and KHAMITOV (1997), (by referring

to KARPENKO 1970 – not seen by us) gives densities like 'up to 1000 specimens in an area of 0.5×2.0 sq km' in the southern regions of Kazakhstan. However, these figures might eventually apply to *tienshanica*, which has a parapatric distribution in this region. These authors (by referring to OKULOV, 1981 – not seen by us) gives lower densities in Western Kazakhstan '(0.86 individuals/ha for clayey arid regions and 0.24 individuals/ha for the sandy ones)'.

Habitat and field observations. The species seems to be restricted to virgin steppe habitats, which also includes stony hill slopes. We observed seven specimens in two localities in the Tarbagatai Mountains in eastern Kazakhstan in September 1998. The habitat was clayey and stony slopes at about 1000 m altitude, with lots of grasslands in-between rocky areas. *Lacerta agilis exigua* was abundant in the habitat.

Taxonomic entity. The populations of *renardi* in lowland former USSR are here treated as a single taxon although in the analyses and text a major division is stressed (west *renardi* and east *renardi*), and which we believe has an evolutionary significance.

In *renardi*, the serum profile is different when comparing individuals of east *renardi* and west *renardi* (Fig. 67).

In scalation characters, a certain east-west difference can be seen. The Kazakh population (Dzherzkazgan) has a higher ventral count (X=146.4) compared to the rest of the examined *renardi* populations (X=142.67 for all populations together). Taken together, the European ones ('west *renardi*') have a mean value of 140.50 ventrals in males, and 143.18 in females, while the Asian ones ('east *renardi*') have a mean value of 143.38 ventrals in males, and 146.38 in females. The highest ventral value (151) is found in a specimen from Tarbagatai Mountains, Eastern Kazakhstan.

The Kazakh population also shows a greater variation in number of supralabials ranging from 17 to 19. Normally *renardi* has rather constantly 18 supralabials (nine per side of head). An increased dorsal scale count on the neck (>21) is meanwhile found in 'west *renardi*'; while 21 is the norm for 'east *renardi*'. As seen above the two subsamples of *renardi* differ also in the number of circumoculars.

Based on our earlier studies together with the present one we have a pattern with two *renardi* lineages with (1) lowland (west) *renardi* together with the West Asian mountain populations, and (2) lowland (east) *renardi* together with the Central Asian mountain populations. If so *Vipera renardi* is paraphyletic unless we separate the eastern and the western *renardi* into two species. As stated earlier in such a scenario the western *renardi* lineage will constitute of a series of sister taxa: *Vipera renardi, V. lotievi, V. eriwanensis*, *V. anatolica* and *V. ebneri*. The eastern

renardi lineage would be represented by a polymorphic taxon divided into a series of subspecies: *Vipera 'r. renardi', V. 'r' tienshanica* and *V. 'r'. parursinii*). In addition, the 'Altai form of *renardi*' belongs to this group.

We have not carried out this taxonomic division here as there was not enough phylogenetic information available for the eastern populations. Further, we do not know whether or not we have a parapatric or sympatric distribution, or just a clinal pattern in characters in the border areas between west and east *renardi*. However, we believe that future studies of these groups will point in the direction of two taxa.

The Orlov Island population may as well be treated as an evolutionary entity, as it has evolved in a unique direction. It is the population with largest body size within the entire complex, and seems to have a rather different ecological niche. KOTENKO (1989) mentions that on the Orlov Island *renardi* feeds also on nestlings of Laridae, ducks and sandpipers, which are most unusual prey items for members of the *ursinii* complex. It has developed a morphology that to a certain extent fits the increased size, such as a higher average number of neck scale rows, etc. Moreover, as indicated by KOTENKO *et al.* (1999), 'among Ukrainian populations only such from Orlov Island has some (genetic) specificity'.

Ukrainian, Russian and Kazakhstan localities and material examined. Ukraine: Island Orlov, Black Sea (MHNG 1354.71–76, 1354.85, 87); Dnepr, Kherson (MHNG 1354.77–84,); Dnepr, Voroschbj? (MHNG 1354.86, 1354.88–90); Dnepr, 18 km E. Kiev (MHNG 1354.91); Ukraine (field no. 230) ZIG.

Azerbaijan: town Shemakha (Shemacha) (ZIG), one specimen.

Russia: Volgograd (Stalingrad), Vaujtzkaja (ZIG 151, 243–244); Saratov (BMNH 93.12.30.4); Altai, Omsk (NRS 1875.809.4736); Sibiria, Omsk (NRS 1875.989.4737); Gov. Tomsk, Zmeinogorsk (BMNH 93.12.30.7); Kislowodsk, North Caucasus (MTKDD 8528–9); Pjatigorsk, North Caucasus (MTKDD 24939).CIS (GNM 1615)Sarepta (ZMK–68106)

Kazakhstan: "Kazakhstan", ZIG; Dzherzkazgan (MTKDD 6041, 8534, 8535, 9017, 9018, 9283, 9534, 9535, 9723, 11387); Sassi-Kul (Sasykkol), N. Aqmola, Kazakhstan (68107); Akterek, Alma Atinsk, Dzambul (ZIG 365–369); Tarbagatai, (N. 47°24'135, E. 81°14'433) (GNM field no. Kaz. 212–216)

Vipera renardi tienshanica ssp. n.
"Tien Shan mountain steppe viper"
(Figs 40–41, 43–45)

Vipera ursinii renardi (part). KRAMER, 1961. Rev. Suisse Zool. 69: 627–722 (the eastern group of his "südöstliche und südwestliche Steppenform").
Vipera ursinii ebneri, SAINT GIRONS 1978 (part.). Rev. Suisse Zool. 85: 565–595.
Vipera ursinii eriwanensis, JOGER 1984 (part.). Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A, Nr. 12, 115 pp.

Holotype: (Fig. 43). (BMNH 93.12.30.9), female.
Terra typica: 'Wernensky Ujesd' (=Almaty), Varnoe, Kazakhstan.
Don.: St. Petersburg Zoological Institute.
Paratypes: KAZAKHSTAN: Almaty (MTKDD 9334, 9536); E.Turkestan (BMNH 93.12.30.10). KIRGIZIA: Chinas (BMNH 93.12.30.8, 79.11.14.270–2); at river Tschu, N. Frunze (MTKDD 13623–4, 14078, 14244). CHINA: Xinjiang, Yining (Kuldja) (BMNH 93.2.17.16–17); Xinjiang, Yining (Kuldja), 26 km north on road of Yining Airport, foothills of Borohoro Shan, 44°00´N, 81°40´E), 1030 m altitude (CAS 197149).

Description. It is a small to medium-sized taxon. Maximum total length in our material is 45.6 cm for males (of which tail length is 5.3 cm), and 40.0 cm for females (tail 4.6 cm).

Head pattern present. Lateral body pattern present in most specimens, but weakly developed. Belly-pattern white. Dark labial sutures present; occipital and postorbital stripes on lateral and dorsal sides of head present; weakly developed bilineate ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings.

Mostly nine supralabials on each side (occasionally from eight to ten) and with the fourth under orbit. Two to six loreals on each side. Nasal mostly normal, upper nasal split normally absent; upper preocular mostly in contact with the nasal; parietals mostly divided (in almost 95% of the cases).

A markedly late reduction of dorsal scale rows (from 21 to 19 rows at an average position exceeding the 80th ventral) i.e. 21 dorsal scale rows on neck, anterior part and midbody, and 17 anterior to anal plate. High number of ventrals (but less than in *renardi*), and high number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 15 specimens of both sexes are as follows: preventrals: 2.20±0.22; ventrals: 135.00±0.76; scale rows on neck: 21.00±0.00; scale rows on midbody: 20.73±0.15; posterior scale rows: 16.93±0.07; level of scale row reduction from 21 to 19 rows (at ventral number, and in%):80.27±2.79 and 59.47±1.98 respectively; supralabials (sum of both sides): 17.33±0.23; sublabials (sum of both sides): 20.80±0.22; circumoculars (sum of both sides): 19.53±0.27; loreals (sum of both sides): 8.87±0.56; crown scales (intercanthals and intersupraoculars): 12.80±0.96; dorsal windings/blotches: 48.20±1.05.

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size
3. Weakly bilineate
4. White belly
5. Lateral blotches and spots present in 80% of the cases
6. Dark sutures on labials
7. Dorsal zigzag band with rounded corners of windings
8. Low number of dorsal windings
9. Nasal without upper nasal split (in around 90% of the cases)
10. Rostral as high as broad
11. A high loreal number
12. More circumoculars
13. Upper preocular in contact with nasal in most of the cases (almost 90% of the cases)

14. Many crown scales
15. Parietals normally fragmented
16. Many supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Many sublabials
20. Fewer mental scales
21. Posterior dorsal scale row reduction, 21 rows on neck and on midbody
22. High ventral number
23. No exposed intersquamose area.
24. High number of subcaudals
25. Alpine/subalpine steppe inhabitant

A taxon in the *Vipera ursinii* complex characterized by an external morphology evolved as typical for mountain taxa of the *ursinii* complex, with small size and whitish belly. It differs from lowland *renardi* by colour and pattern (throat, supralabials, belly, lateral sides), size, ecology and all Asian mountain taxa by a combination of scalation characters (e.g. shape of the rostral plate; from *ebneri* in ventral and subcaudal numbers). It differs from European mountain *ursinii* by having 21 midbody scale rows and a higher number of supralabials.

Karyotypes of '*Vipera ursinii renardi*' (='*tienshanica*') from northern Tien Shan in Kazakhstan are described as 2n = 36, NF = 50 (TOKTOSUNOV *et al.* 1992). The karyotype is identical to *V. renardi* from Russia (see above). Both differ from west European *ursinii* in W-chromosome morphology.

The morphological description of *V. u. ebneri* by SAINT GIRONS (1978) and by DELY and STOHL (1989a) are based on populations here separated as *eriwanensis*, *ebneri* and *tienshanica*.

The external morphology and cranial osteology of two specimens from the Almaty (=Alma-Atinsk) population are discussed by DELY and STOHL (1989*b*).

Description of holotype. An adult female (Fig. 43), total length 394 mm, tail 35 mm, latter equal to 8.9% of total length. Length of head (from posterior border of parietals to tip of snout) 11.5 mm, breadth of head (at position of eyes) 8.4 mm, size of eye horizontally 2.5 mm and vertically 2.0 mm, distance between eye and lip 2.0 mm. Anterior head flat and covered with rather large scales or plates. Two large supraoculars and 1 large frontal plate on top of head, parietals fragmented, frontal separated from supraoculars by 2 smaller scales on each side, 1 canthal and 1 supranasal scale on each canthus rostralis, and a single apical; 4 intercanthals and 5 intersupraoculars. Height/depth of rostral 3.0/2.9 mm, it is bordering 2 supralabials, 2 internasals and the apical; eye surrounded by 11 circumoculars on each side, 5 loreals on right side and 4 on left, upper preocular in contact with nasal on both sides, nasal undivided at upper edge, 9 supralabials, with forth below eye, and 11 sublabials on each side, 4 second chinshields bordering anterior ones and 3 scales in the mental row.

Three preventrals and 137 ventrals, 27+1 subcaudals, 21 dorsal scale rows at midbody and on neck one head-length behind the head, 17 dorsal scalerows one head-length anterior to anal, scale reduction from 21 to 19 dorsal scale rows at ventral 96.

Dorsal pattern consisting of a zigzag band with 52 windings, lateral body pattern reduced and consists of short narrow black longitudinal stripes or spots. Head pattern consists of 2 dark oblique bands, which do not unite, and a posterior band from eye to corner of mouth, labial pattern consisting of more or less pronounced band on the labial sutures, ground colour light brown with dorsal pattern dark brown and with black edged outer turns, ventral side whitish, throat light.

Variation (see Tables 5 to 36).

Distribution (Fig. 72). It is found in Kirgizia, eastern Uzbekistan (BOGDANOV 1960), northern parts of Tadjikistan (SAID-ALIEV 1979), part of Southern Kazakhstan, and parts of China (Xinjiang). In parts of northern Xinjiang, China (Nilka Xian and Xinyuan Xian (Künes) *parursinii* occurs and this taxon differs markedly from *tienshanica* and other "*ursinii*" s. l. populations in having only 19 dorsal midbody scale rows (see below, and ZHAO & JIANG 1979). According to DJUSEBAJEVA and KHAMITOV (1997), *'Vipera ursinii'* (probably both *renardi* and *tienshanica)* is frequent in 'the ravine between Chu and Ily Rivers, Trans-Ily Alatau Range of Tien-Shan Mountains, southeastern and northeastern slopes of Karatau Mountains, and western slopes of Dzungar Alatau Mountains'.

The populations here defined as *tienshanica* have earlier been referred to *eriwanensis* or *ebneri* (s. l.) (SAINT GIRONS 1978, JOGER 1984, DELY & STOHL 1989, BARON *et al.* 1993). It is parapatric with *renardi* in the Tien Shan region in Kazakhstan.

Habitat. The habitat is mountain meadows with extensive grass vegetation (own obs.) to more dry mountain steppe (Fig. 42).

Taxonomic entity. This taxon consists of the "eastern *renardi*" (sensu MÉHELY 1911); part of the "Südöstliche (und südwestliche) Steppenform" (sensu KRAMER 1961 (part.)); 'population 3' of *Vipera ursinii eriwanensis*, sensu JOGER (1984); and population C of *Vipera ursinii eriwanensis*, sensu BRODMANN (1987). It also consists of the Chinese populations considered as *Vipera ursinii renardi* by ZHAO and JIANG (1979).

Kirgizian, Kazakhstan and Chinese localities and material examined. Kazakhstan: Almaty (MTKDD 9334, 9536); Wernensky (=Almaty) Ujesd, Varnoe, E.Turkestan (HOLOTYPE – BMNH 93.12.30.9); (BMNH 93.12.30.10).

Uzbekistan: Chinas (BMNH 93.12.30.8, 79.11.14.270–2);

Kirgizia: at river Tschu (Chu), N. Frunze (Bishkek) (MTKDD 13623–4, 14078, 14244).

China: Xinjiang, Yining (Kuldja) (BMNH 93.2.17.16–17); Xinjiang, Yining (Kuldja), 26 km north on road of Yining Airport, foothills of Borohoro Shan,

44°00′N, 81°40′E), 1030 m altitude (CAS 197149). Yumin Xian (CIB 765080, 765220, 765222); Tacheng Xian (Qoqek) (CIB 645183).

Vipera renardi parursinii ssp. n.
"Xinjiang mountain steppe viper"
(Figs 46–52)

Holotype: CIB 775157 (Fig. 46)

Terra typica: Nilka Xian, northern Xinjiang, China.

Holotype. CIB 775157. Leg. Zhao Ermi 1975–06–10

Paratypes: 25 specimens from the type locality (CIB 765255, 765259, 765260, 775131–132, 775136–137, 775143, 775148, 775153, 775155, 775164, 775175, 775177, 775180, 775190, 775194, 775196–197, 775199, 775213, 775237–238, 775242, 775244); 5 specimens from Xinyuan Xian (CIB 745092–096). Leg. ZHAO ERMI 1976–1977.

Description. It is a small to medium-sized taxon. Maximum total length in our material is 41.5 cm for males (of which tail length is 5.3 cm), and 35.4 cm for females (tail 3.5 cm).

Head pattern and lateral body pattern present in most specimens. Belly-pattern white. Dark labial sutures developed; occipital stripes of head present; not bilineate ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings.

On average near nine supralabials on each side (occasionally from eight to eleven) and with the fourth under orbit. Three to six loreals on each side. Nasal normal without an upper nasal split; upper preocular in contact with the nasal; parietals divided (totally fragmented in almost all cases (Figs 49, 50)).

An early reduction of dorsal scale rows (from 21 to 19 rows at an average position near the ninth ventral), i.e. 19 dorsal scale rows from neck to midbody, and 17 anterior to anal plate. Relatively high numbers of ventrals and subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 30–31 specimens of both sexes are as follows: preventrals: 2.26±0.11; ventrals: 135.83±0.43; scale rows on neck: 19.13±0.08; scale rows on midbody: 19.26±0.11; poste-



Fig. 46. Male holotype of *V. renardi parursinii* ssp. n. (CIB 775157), Nilka Xian, Xinjiang

rior scale rows: 16.97±0.03; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 8.81±0.74 and 6.47±0.56 respectively; supralabials (sum of both sides): 17.67±0.19; sublabials (sum of both sides): 19.32±0.19; circumoculars (sum of both sides): 20.07±0.13; loreals (sum of both sides): 10.63±0.21; crown scales (intercanthals and intersupraoculars): 12.26±0.35; dorsal windings/blotches: 54.77±0.55.

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small to medium size
3. Non-bilineate ground colour
4. White belly
5. Small lateral blotches and spots present
6. Dark sutures on labials
7. Dorsal zigzag band with rounded corners of windings
8. Medium number of dorsal windings
9. Upper nasal split absent (in 90% of the cases)
10. Rostral as high as broad
11. A high loreal number
12. Many circumoculars
13. Upper preocular in contact with nasal
14. Many crown scales
15. Parietals fragmented
16. Many supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Medium number of sublabials
20. Low number of mental scales
21. Early dorsal scale row reduction, 19 rows on neck and midbody
22. High ventral number
23. No exposed intersquamose area
24. High number of subcaudals
25. Alpine/subalpine steppe inhabitant

A species of the *Vipera ursinii* complex characterized by an external morphology evolved as typical for mountain taxa of the *ursinii* complex; similar to European mountain populations (*ursinii, macrops*) in some characters and to *renardi* and Asian mountain populations (*eriwanensis*) in others but differs from both in combination of characters. It differs from parapatric *renardi* by having 19 midbody scale rows with an very early dorsal scale row reduction (X=at 8th ventral number) (21 in *renardi*, with mean scale reduction at 100th ventral number); a lower number of ventrals, which are whitish in colour. It differs from European

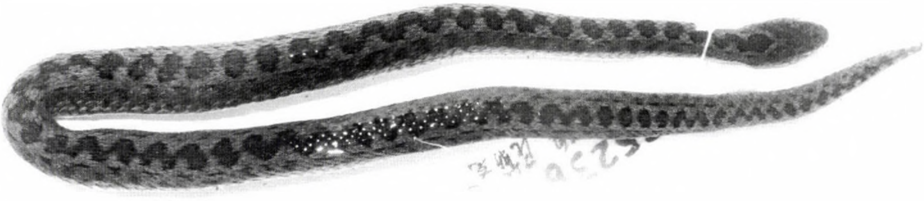


Fig. 47. Male paratype of *V. renardi parursinii* ssp. n. (CIB 775238), Nilka Xian, Xinjiang

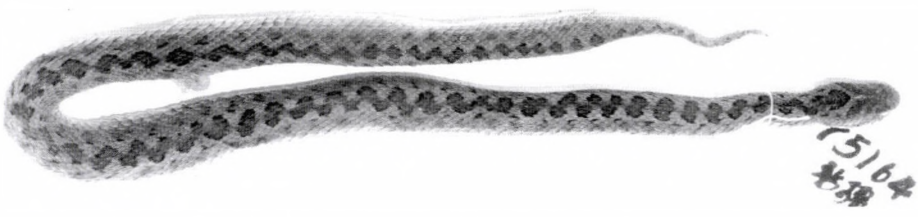


Fig. 48. Male paratype of *V. renardi parursinii* ssp. n. (CIB 775164), Nilka Xian, Xinjiang

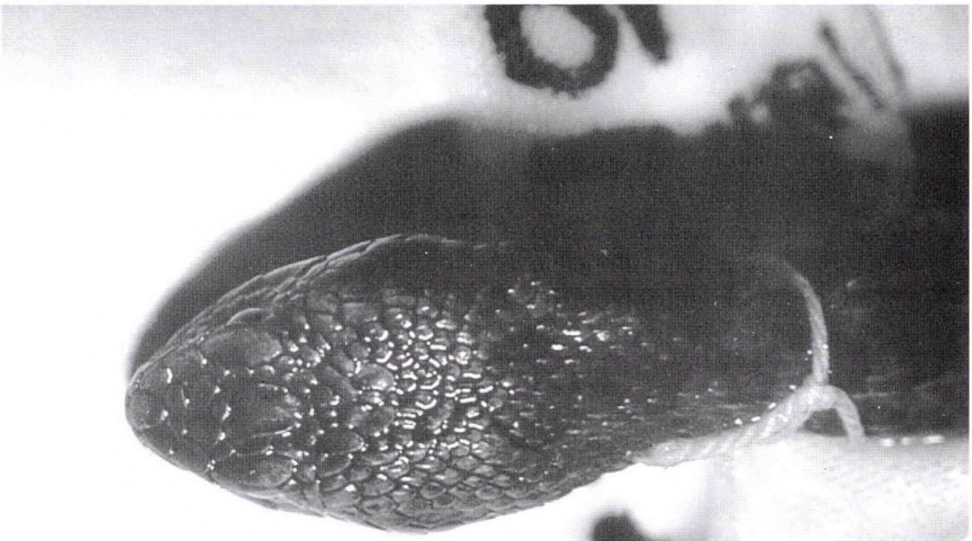


Fig. 50. Head of paratype *V. renardi parursinii* ssp. n. (CIB 775190), Nilka Xian, Xinjiang. Dorsal view

mountain *ursinii* by having a high number of supralabials. It is separated from most taxa by having almost totally fragmented parietals (replaced by a mean number of eight scales), broad banded black suture on all supralabials (Fig. 51, 52), lateral body pattern reduced to short longitudinal stripes (extreme uppermost part of the original lateral blotch characteristic for other *ursinii* s. l.), dorsolateral longitudinal lines on outermost parts of ventrals, bulging labial region, double postocular rows.

The presence of an interparietalia, that DELY & STOHL (1989a) considered as unique for *anatolica* was found in all examined specimens (N=31) of *parursinii*.

Description of holotype. An adult male (Fig. 46), total length 321 mm, tail 49 mm, latter equal to 15.3% of total length. Length of head (from posterior border of parietals to tip of snout) 11.2 mm, breadth of head (at position of eyes) 6.7 mm, size of eye horizontally 2.7 mm and vertically 1.8 mm, distance between eye and lip 2.1 mm. Anterior head flat and covered with rather large scales or plates. Two large supraoculars and 1 large frontal plate on top of head, parietals fragmented (X=7; range 4–12 scales), frontal separated from supraoculars by 3 smaller scales on each side, 1 canthal and 1 supranasal scale on each canthus rostralis, and a single apical; 5 intercanthals and 7 intersupraoculars. Height/depth of rostral 2.6/2.5 mm, it is bordering 2 supralabials, 2 internasals and the apical; eye surrounded by 11 circumoculars on right side and 10 on left, 6 loreals on right side and 5 on left, upper preocular in contact with nasal on both sides, nasal undivided at upper edge, 9 supralabials, with forth below eye, and 9 sublabials on right and 10 on left side, anterior supralabials not much enlarged compared to posterior ones, 4 second chinshields bordering anterior ones and 4 scales in the mental row.

Three preventrals and 134 ventrals, 34+1 subcaudals, 19 dorsal scale rows at midbody and on neck one head-length behind the head, 17 dorsal scalerows one head-length anterior to anal, scale reduction from 21 to 19 dorsal scale rows at ventral 7.

Dorsal pattern consisting of a zigzag band with 58 windings, lateral body pattern reduced and consists of short, narrow longitudinal stripes. Head pattern consists of 2 dark oblique bands, which do not unite, and a posterior band from eye to corner of mouth, labial pattern consisting of pronounced band on all labial sutures, ground colour light brown with dorsal pattern dark brown, ventral side whitish, throat light. Dorsoventral longitudinal lines on outer edge of ventrals.

Variation (see Tables 5 to 36).

Distribution (Fig. 72). It is distributed in parts of northern Xinjiang (Nilka Xian and Xinyuan Xian (Künes)), China.

Comments. A colour photo of a live specimen from the type locality area at Nilka Xiang was published by ZHAO & ADLER (1993). The habitat can be described as hilly dry meadows.

Taxonomic entity. This is the local form of *ursinii* described by ZHAO and JIANG (1979) as *V. u. ursinii* (part.) from northern Xinjiang. It differs conspicuously from other "*renardii*" s.lat. populations (=Central Asian "*ursinii*") by having only 19 dorsal midbody scale rows and from east *renardi* and the 'Altai form of *renardi*' by a low ventral count (ZHAO & JIANG 1979). We consider *Vipera renardi parursinii* as a well-defined taxon, not close to any other sample examined here.

Chinese localities and material examined. China: Nilka Xian, northern Xinjiang, (Holotype-CIB 775157; Paratypes- CIB 765255, 765259–60, 775131–132, 775136–137, 775143, 775148, 775153, 775155, 775164, 775175, 775177, 775180, 775190, 775194, 775196–197, 775199, 775213, 775237–238, 775242, 775244); Xinyuan Xian, northern Xinjiang (CIB 745092–096).

'Altai form of *renardi*'
"Altai steppe viper"
(Fig. 53)

TUNIYEV, NILSON et ANDRÉN, (in prep).

Description. It is a taxon within the *renardi* group, and in the same way living in lowland areas (150–450 m alt.). However, size and morphological characteristics developed as in alpine/subalpine taxa within this complex.

It is small sized (> 40 cm). None of 36 examined specimen was 40 cm or larger, and this general size was also the case for 40 to 50 specimens observed in Kazakhstan in 1997. The wide ranging and allopatric *Vipera renardi* reaches 60 to 70 cm.

The belly in the 'Altai form of *renardi*' is white or mixed white and black, where light colours predominate. *Vipera renardi* has a blackish belly.

It has a laterally pointed zigzag band, or transverse bands along its back (*renardi* has a typical undulating, brownish and black-edged dorsal band).

It is a small taxon of the *Vipera ursinii* s.lat. complex, and has its closest affinity to *renardi*. Maximum total length in our material is 38.8 cm for males (of which tail length is 5.0 cm), and 39.9 cm for females (tail 3.6 cm).

Head pattern and lateral body pattern is present in most specimens. Belly-pattern whitish. Dark labial sutures developed in males, absent or weakly developed in females; occipital stripes of head present; ground colour not bilineated; dorsal pattern consists of a pronouncedly developed zigzag band with pointed or slightly rounded corners of windings, or transverse stripes. Lateral spots present, being single, squarish and tilted. Ground colour uniform brownish, with a denser staining at lower lateral parts of body.

On average nine supralabials on each side (occasionally ten) and with the fourth under orbit. Two to six loreals on each side. Nasal normal, without an upper nasal split; upper preocular mostly in contact with the nasal; parietals fragmented, divided or undivided.

Reduction of dorsal scale rows from 21 to 19 rows at an average position between ventrals 73 to 98, i.e. 21 dorsal scale rows from neck to midbody, and 17 anterior to anal plate. A high number of ventrals makes the dorsal scalerow reduction comparatively early.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 11 specimens of both sexes are as follows: preventrals: 2.18±0.12; ventrals: 146.36±0.72; scale rows on neck: 21.00±0.00; scale rows on midbody: 20.82±0.12; posterior scale rows: 17.00±0.00; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 90.57±3.37 and 62.29±2.53 respectively; supralabials (sum of both sides): 18.27±0.14; sublabials (sum of both sides): 20.09±0.21; circumoculars (sum of both sides): 19.00±0.27; loreals (sum of both sides): 8.46±0.81; crown scales (intercanthals and intersupraoculars): 12.50±1.16; dorsal windings/blotches: 65.82±1.79.

Diagnosis. A taxon within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small to medium size
3. Non-bilineate ground colour
4. Whitish belly
5. Small lateral blotches and spots present
6. Dark sutures on labials in males
7. Dorsal zigzag band with pointed corners of windings, or with transverse bars
8. High number of dorsal windings
9. Upper nasal split absent
10. A squarish rostral
11. A variable loreal number
12. Many circumoculars
13. Upper preocular in contact with nasal
14. Medium number of crown scales
15. Parietals fragmented or not
16. Nine supralabials
17. Posterior supralabials of the same size as anterior ones
18. Fourth supralabial below orbit
19. Nine or ten sublabials
20. Four mental scales
21. Somewhat early dorsal scale row reduction, 21 rows on neck and occasionally only 20 at midbody
22. High ventral number
23. No pronounced exposed intersquamose area.
24. High number of subcaudals
25. Foothill steppe inhabitant

A lowland or foothill taxon of the '*Vipera ursinii* complex' characterised by an external morphology normally evolved as typical for mountain taxa of the *ursinii* complex. It is similar to European mountain populations (*ursinii, macrops*) in some characters and to *renardi* and Asian mountain populations (*eriwanensis*) in others, but differs from both in combination of characters.

It is special in being the smallest taxon, and having the highest number of ventrals within the entire complex. It is also special in being a lowland dweller with colour and scalation characteristics typical for mountain taxa, and in having a pronounced sexual dimorphism in labial pattern and loreal number.

It differs from allopatric (parapatric?) *renardi* by having an earlier dorsal scale row reduction, whitish ventrals, sharply bent or transversely banded dorsal pattern, and by being small.

It differs from European Mountain *ursinii* by having a high number of supralabials and ventrals. It is separated from most taxa by having almost totally fragmented parietals (replaced by a mean number of eight scales), and banded black suture on supralabials weakly developed or absent and a different pattern. The lateral body pattern is reduced to tilted squarish rhombic spots, and dorsal scales are pronouncedly keeled. No interparietalia.

Variation (see tables).

Distribution (Fig. 72). It is distributed in Altai mountain range in lower sections with dry climate. We observed it in 1997 and 1999 at three localities in soutwestern Altai Mountains and in one locality in the Saur Mountains in Eastern Kazakhstan, near the Chinese border. Specimens mentioned by BORKIN *et al.* (1990) and ANANJEVA *et al.* (1997) from the Altai Mountains in the Chinese–Mongolian border areas most probably belong to the same taxon. In addition, we have seen Chinese material of this taxon from the Chinese section of Altai (Habahe Xian).

Habitat and field observations. The species seems to be connected to stony and rocky slopes, often near water in lowland or foothill areas. Surrounding areas covered by sparse grass vegetation. *Lacerta agilis exigua, Natrix natrix scutata, Elaphe dione, Coluber spinalis* and *Akistrodon halys halys* occurred in the same, somewhat moist microhabitat. *Alsophylax pipiens* and *Phrynocephalus helioscopus* were sympatric, but not syntopic.

Taxonomic entity. This is a well-defined taxon. It has currently been included in *Vipera renardi* s. l. A more detailed investigation is in preparation elsewhere.

Kazakhstan and Chinese localities, and material examined. Kazakhstan: 16 specimens from Kalgir (Kalchir village)(N. 48° 12,260', E. 85° 10,168'). (1997 – GNM Re.ex field no. Kz 221–230; 1999 – GNM Re.ex field no. Kz 416–419, leg GÖRAN NILSON, CLAES ANDRÉN); 19 specimens from Slavijanka (N. 48°49,333', E. 83° 33,100') (GNM Re.ex. field no. Kz 405–412, leg. GÖRAN NILSON, CLAES ANDRÉN, 1999–06–30; ZISP, field no. 6302 –6313, leg. NIKOLAI ORLOV, ANDREJ BARABANOV 1999–06–30). One specimen, 50 km E. Kurchum, 30 km E. Voznesenka Village (N. 48°27,747', E. 84° 08,072')(ZISP field no. 6298) leg. NIKOLAI ORLOV. Saur Mountains, (N. 47°25'731, E. 85°17'191) (GNM field no. Kaz. 421+12 juv.) leg. GÖRAN NILSON.

China: Habahe Xian (Kaba) (CIB 765210–13, 765215–16).

Vipera anatolica EISELT et BARAN, 1970
"Anatolian mountain steppe viper"
(Fig. 54)

Vipera ursinii anatolica EISELT et BARAN, 1970
Terra typica: Ciglikara Ormani, Kuhu Dagh Mountains, prov. Antalya, South Turkey. Holotype: Sistematik Zooloji Enstitüsü, Bornova-Izmir, no. 170. 1969. Leg. A. BUDAK, 1969.
Vipera ursinii ursinii, SAINT GIRONS 1978 (part.). Rev. Suisse Zool., 85: 565–595.
Vipera anatolica, JOGER *et al.* 1992. Proc. Sixth Ord. Gen. Meet. S.E.H., Budapest 1991 239–244.

Description. It is a small to medium sized taxon. Maximum total length in our small series of females is 43.4 cm, of which tail length is 3.7 cm.

Head pattern present. Lateral body pattern present. Belly-pattern white. Dark labial sutures very weak or lacking (in three of four investigated specimens); occipital stripes of head present; no bilineate ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings.

On average eight supralabials on each side (occasionally from seven to nine) and with the fourth under orbit. Three to six loreals on each side. Nasal mostly normal, upper nasal split present in two thirds of the cases; upper preocular in contact with the nasal; parietals often divided (in three of four specimens).

An early reduction of dorsal scale rows (from 21 to 19 rows at an average position at the eleventh ventral) i.e. 21 dorsal scale rows on neck posterior of the head, but 17 on anterior part and

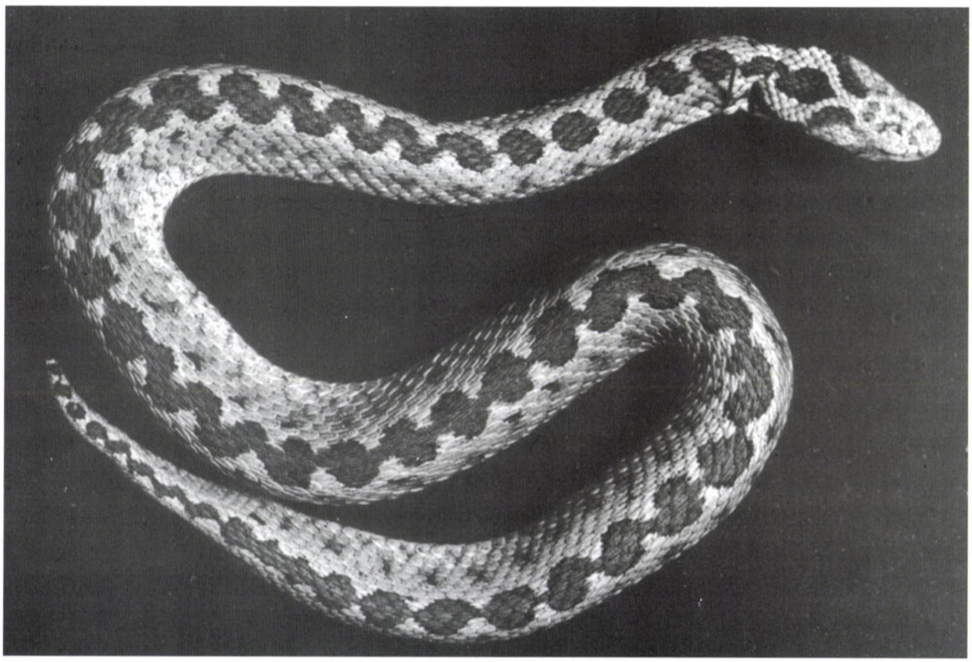


Fig. 54. Female of *V. anatolica* (ZIG) from the type locality (Ciglikara, prov. Antalya, Turkey)

midbody, and anterior to anal plate (16 in one specimen). Low number of ventrals, and low number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 3–4 specimens of both sexes are as follows: preventrals: 2.00±0.41; ventrals: 118.25±0.10; scale rows on neck: 19.33±1.20; scale rows on midbody: 19.33±1.20; posterior scale rows: 16.75±0.25; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 11.00±2.89 and 9.00±2.31 respectively; supralabials (sum of both sides): 16.00±0.82; sublabials (sum of both sides): 21.00±0.71; circumoculars (sum of both sides): 18.50±0.87; loreals (sum of both sides): 9.50±1.26; crown scales (intercanthals and intersupraoculars): 13.50±1.32; dorsal windings/blotches: 38.00±2.31.

A taxon of the *Vipera ursinii* complex characterized by a unique serum albumin. Genetically most similar to the Asian *eriwanensis* and *renardi* branch, together with which it forms an evolutionary lineage of common ancestry (JOGER *et al.* 1992).

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size
3. Not bilineate
4. White belly
5. Lateral blotches and spots present
6. Normally no dark sutures on labials
7. Dorsal zigzag band with rounded corners of windings
8. Very low number of dorsal windings (42 or fewer)
9. Upper nasal split present (in around two thirds of the cases)
10. A high and narrow rostral
11. A high loreal number
12. Medium to more circumoculars
13. Upper preocular in contact with nasal
14. Many crown scales
15. Parietals normally not fragmented
16. Medium number of supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Many sublabials
20. Medium number of mental scales
21. Posterior neck dorsal scale row reduction, 21 rows on upper neck, 17 on anterior part and midbody
22. Low ventral number
23. No exposed intersquamose area.
24. Low number of subcaudals
25. Alpine/subalpine steppe inhabitant

A taxon in the *Vipera ursinii* complex characterized by an external morphology evolved as typical for mountain taxa of the *ursinii* complex, with small size

and whitish belly. It differs from all other taxa in a very low number of windings in the dorsal zigzag band (34–42), and from most in the low number of ventrals and subcaudals. It differs from *renardi* as well as from Asian mountain *ursinii* (except *parursinii*) by having 19 midbody scale rows. From all European lowland and mountain *ursinii* it further differs in the shape of the rostral, high loreal and sublabial number, low number of ventrals and subcaudals.

Distribution (Fig. 70). Anatolian alpine meadow viper restricted to Ciglicara in the Kohu Dag Mountains, southwest of Elmali in province Antalya, Southern Turkey. Reports on three specimens from this locality has been published (EISELT & BARAN 1970, BILLING 1985, SIGG 1987). A nearby locality has also been reported (SAINT GIRONS 1980, JOGER 1984), but without reference to observed specimens. One specimen (NMNH 4000), without exact locality, was collected in Turkey during the first part of the nineteenth century by Boie.

Estimated population size. One additional specimen has been in captivity in Europe (HECKES, in litt.) and which we have been able to examine (courtesy of SATTLER and HECKES). In total, three of the five specimens known from literature, museum collections (including the paratype) or in private hands have been examined together with literature data of the holotype. The low number of observed specimens is probably due to a low density due to the heavily sheep-grazed habitats, but partly also that the remote places that certainly constitute its habitat are difficult to get access to.

Comments. The morphology of the first (and to our knowledge presently the only) known male of this taxon was discussed by BILLING (1985) and SIGG (1987). Photos of this live specimen were published by these authors, and by BRODMANN (1987).

Field observations. The Ciglikara area was visited a few times and the habitat is a mixture of mixed coniferous forests (*Cedrus libani, Juniperus excelsa, J. foetidissima*) with small grass meadows on limestone ground (dolines), which is a part of the *anatolica* habitat (EISELT & BARAN 1970) (Fig. 55). Additional notes of the habitat can be found in SIGG (1987) and NILSON *et al.* (1988). Sympatric but not always syntopic species in the region are *Bufo v. viridis, Testudo graeca ibera, Ablepharous k. kitaibelli, Lacerta oertzeni budaki, Laudakia stellio daani, Natrix natrix persa, Coluber najadum dahli, C. caspius, Eirenis modestus, Vipera xanthina*.

Taxonomic entity. *Vipera anatolica* is a well-defined taxon, not close to any other here-examined sample. However, it has occasionally been treated as a part of a larger assembly of taxa (as here defined) under the *name Vipera u. ursinii* (s. l.). This taxon has been included in the nominal subspecies (*V. u. ursinii*), and thereby considered as having closest affinity to Balkan, Italian and French mountain popu-

lations. Besides the demonstrated phylogenetic relation to the more eastern Asian populations, the late Cenozoic evolution of the Aegean region clearly shows that the Anatolian and Balkan mountain populations never can have had direct contact. At most, they could be related through some northern lowland form (like *moldavica*). If this was true '*Vipera u. ursinii*' (s. l.) would be a paraphyletic taxon.

Turkish localities and material examined. Turkey: Ciglikara, prov. Antalya (Holotype – from literature; NMW 19559 – Paratype; ZIG – one unregistered specimen ('from terra typica or 20 km away')); "Turkey" (NMHN 4000);

Vipera eriwanensis (REUSS, 1933)
"Armenian mountain steppe viper"
(Fig. 56)

Acridophaga renardi eriwanensis TH. REUSS, 1933, Nachr. Bl. Aquar. Terrar. Ver. Berlin 1933: 372–373. – Terra typica: Erivan (at 2000 m altitude), Armenia. Type: lost. Illustration was published by REUSS in 1935, and a diagnosis was given. An illustration published already in 1929 is supposed to show the type alive (SOCHUREK, in litt.).

Vipera ursinii renardi (part.) KRAMER 1961. Rev. Suisse Zool. 69: 627–722 (the western group of his "südöstliche und südwestliche Steppenform").

Vipera ursinii ebneri (part.) SAINT GIRONS 1978. Rev. Suisse Zool. 85: 565–595.

Vipera ursinii eriwanensis, JOGER 1984. Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A, Nr. 12, 115 pp.

Vipera eriwanensis, HÖGGREN *et al.* 1993. Herpetological Natural History 1(2): 11–19.

Comments. The description is based on one specimen, but the type series seems to consist of more than a single specimen as different individuals are depicted in the 1929 and 1935 papers by REUSS. All specimens are lost, and the description is short and not exclusive for the *ursinii* complex. The name *eriwanensis* has been referred to the single taxon occurring in close vicinity of the town Erivan, i.e. *ursinii* s. l. (=*renardi*, in earlier literature). JOGER (1984) raised it to valid level by stating that "Though REUSS' type specimen is lost, there can be no doubt about its identity, as no similar viper occurs in the Erewan area". However, *Vipera darevskii* (see below) which has some morphological affinity is distributed in northwest Armenia, although not close to Erewan. In the absence of any type material, and for reasons of stability we have earlier, together with BORIS TUNIJEV and NIKOLAI ORLOV, considered it appropriate to select a neotype of *Acridophaga (renardi) eriwanensis* (=*Vipera eriwanensis*) from the Yerevan area: GNM, Re. ex.: 5158 (NILSON *et al.* 1999*b*) (see below).

Description. It is a small to medium-sized taxon. Maximum total length in our material is 44.7 cm for males (of which tail length is 5.7 cm), and 50.1 cm for females (tail 6.3 cm).

Head pattern present, while lateral body pattern absent or more weakly developed. Belly-pattern white. Labial sutures absent in half of the specimens or weekly developed; occipital and postorbital stripes on lateral and dorsal sides of head present; weakly developed bilineate ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings.

Normally nine supralabials on each side (occasionally from eight to ten) and with the fourth under orbit. Two to nine loreals on each side. Nasal mostly normal, occasionally with an upper nasal split (in less than 30% of the cases); upper preocular mostly not in contact with the nasal; parietals occasionally divided (in around 20% of the cases).

A markedly late reduction of dorsal scale rows (from 21 to 19 rows at an average position near the 95th ventral) i.e. 21 dorsal scale rows on neck, anterior part and midbody, and 17 anterior to anal plate. High number of ventrals. High number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 47 specimens of both sexes are as follows: preventrals: 2.00±0.10; ventrals: 137.34±0.37; scale rows on neck: 21.06±0.05; scale rows on midbody: 21.09±0.10; posterior scale rows: 17.00±0.03; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 94.17±1.00 and 68.57±0.67 respectively; supralabials (sum of both sides): 18.02±0.08; sublabials (sum of both sides): 19.94±0.21; circumoculars (sum of both sides): 18.68±0.33; loreals (sum of both sides): 10.13±0.40; crown scales (intercanthals and intersupraoculars): 13.11±0.35; dorsal windings/blotches: 65.32±0.80.

A taxon of the *Vipera ursinii* complex characterized by a unique serum albumin, most similar to the serum albumin pattern of *renardi*, and more so to the eastern population of this taxon (Fig. 67) (see also JOGER *et al.* 1992, NILSON *et al.* 1993). Also by immunological results perhaps most similar to this lowland taxon, as is also indicated by electrophoretic studies of isoenzyme (NILSON *et al.* 1994, 1995).

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size
3. Weakly bilineate
4. White belly
5. Lateral blotches and spots missing in almost 40% of the cases
6. Normally dark sutures on labials in half of the cases, and weakly on lateral and dorsal sides of head, including occipital and postorbital stripes
7. Dorsal zigzag band with rounded corners of windings
8. A high number of dorsal windings
9. Nasal with an upper nasal split in less than one third of the cases
10. A high and narrow rostral
11. A high loreal number
12. Medium to high number of circumoculars
13. Upper preocular separated from nasal in most of the cases
14. More crown scales
15. Parietals normally not fragmented
16. Many supralabials
17. Posterior supralabials not very much smaller than anterior ones

18. Fourth supralabial below orbit
19. Many sublabials
20. More mental scales
21. Posterior dorsal scale row reduction, 21 rows on neck and on midbody
22. Comparatively high ventral number
23. No exposed intersquamose area
24. Higher number of subcaudals
25. Alpine/subalpine steppe inhabitant

External morphology evolved as typical for alpine taxa of the *ursinii* complex; similar to *ebneri, lotievi* and to the *tienshanica* in various characters, but differs from all in combination of characters (ventral numbers, labial colour, head scalation characters). Differs from alpine European (and Asian *anatolica* and *parursini*) in number of midbody scale rows.

Description of neotype (from NILSON *et al.* 1999*b*). The neotype is an adult male (GNM Re. ex. 5158) collected on the mountain Ara-Iler, Armenia, to the north of Yerevan in May 1972. Donated by Zoological Institute, St. Petersburg to Göteborg Natural History Museum. Total length 401 mm, tail 49 mm, latter equal to 12.2% of total length. Length of head (from posterior border of parietals to tip of snout) 11.4 mm, breadth of head (at position of eyes) 8.8 mm, size of eye horizontally 2.2 mm and vertically 1.7 mm, distance between eye and border of mouth 1.9 mm. Anterior head flat to weakly concave and covered with rather large scales or plates. Two large supraoculars and 1 large frontal plate on top of head, parietals unfragmented, frontal separated from supraoculars by one longer anterior and one smaller posterior scale on each side, 1 canthal and 1 supranasal scale on each canthus rostralis, and a single apical; 5 intercanthals and 5 intersupraoculars. Height/depth of rostral 3.2/2.6 mm, it is bordering 2 supralabials, 2 internasals and the apical; eye surrounded by 10 circumoculars on each side, 4 loreals on right side and 5 on left, upper preocular separated from nasal on both sides, nasal undivided at upper edge, 9 supralabials, with fourth below eye, and 10 sublabials on each side, anterior supralabials not much enlarged compared to posterior ones, 4 second chinshields bordering anterior ones, and 3 and 4 scales on right and left side respectively in the mental row.

Two preventrals and 136 ventrals, 37+1 subcaudals, 21 dorsal scale rows at midbody and on neck one head-length behind the head, 17 dorsal scale rows one head-length anterior to anal, scale reduction from 21 to 19 dorsal scale rows at ventral 97.

Dorsal pattern consisting of a zigzag band with 70 windings, lateral body pattern weakly developed and consisting of short narrow longitudinal stripes. Head pattern consists of 2 dark oblique bands, which do not unite, but are just in contact with the dorsal band on both sides. A posterior band from eye to corner of mouth, labial pattern consisting of weak bands on all labial sutures, ground colour light brown with dorsal pattern dark brown and black, ventral side light, but with blackish marbling, throat light.

Distribution (Fig. 70). The range of this taxon is restricted to the Armenian plateau, which includes the political regions of Armenia, Western Azerbaijan, and eastern Turkey (Kars and Erzurum provinces) (CHERNOV 1939, BARAN 1976, BASOGLU & BARAN 1980, JOGER 1984, NILSON *et al.* 1988). Besides the single re-

cord from the Palandöken Mountains, south of Erzerum, Turkey (EISELT 1976) the total distribution is north of the Arax river.

In the earlier literature, all transcaucasian meadow vipers have been referred to *renardi*, as is also the case by ALEKPEROV (1978) for the Azerbaijan populations. This is partly true as *renardi* actually occurs in the north of that country (see discussion under the *renardi* section and under Results), but the situation is more complicated.

However, *eriwanensis* is widely distributed in the most western mountain areas of Azerbaijan (ALIEV & GANIEV 1985). We observed several specimens in Armenia on the border mountains between Armenia and Azerbaijan (Aragunyi ridge) in June 1992. It is also frequent in the Karabakh plateau (2000–3000 m altitude) (ALEKPEROV 1982). All these habitats are dry high mountain meadows. It is also reported from 2500 m altitude at lake Kanligel, Nakhitshevan (as *renardi* part. – ALEKPEROV 1978, or as *ursinii* – ALEKPEROV 1982).

TEYNIE (1987) and NILSON *et al.* (1988) further discuss the Turkish localities.

Estimated population size. Local density of three to four snakes per hectare is given for the Karabakh plateau situated in Southwestern Azerbaijan (ALEKPEROV 1982). We found about ten specimens per hectare of good habitat both in Armenia (Arailer mountain) and in eastern Turkey (Kagizman region).

Field observations. We observed *eriwanensis* at six different places in eastern Turkey (Kars province) and Armenia at several occasions. It was abundant at all visited places. The habitats, normally at between 1000 and 2000 m altitude, were covering rather large areas as much of this region is situated on the Armenian high plateau (Fig. 57). In most places, it was sympatric with *Coronella a. austriaca*. In the Arpacay region, Kars province, however, the two species were very abundant in different valleys. Here *Natrix natrix persa, N. tesselata, Lacerta v. valentinii* and *Rana cameranoi* also occurred. In the Sarakamis region *Lacerta agilis brevicaudata* and *L. uzzelli* were also observed in sympatry. Both at Mt. Arailer and Mt. Aragatz in Armenia, *Elaphe hohenackeri* was sympatric as well, besides *Natrix tessellata, Lacerta raddei nairensis, Lacerta media, Coluber n. najadum* and *Vipera r. raddei*. Locally, *Rana cameranoi* was also frequent. At Sevan lake, on the Azerbaijan border in Armenia, *Lacerta strigata, Lacerta agilis brevicaudata, Lacerta armeniaca, Laudakia caucasia, Coronalla a. austiaca* and *Natrix tessellata* were frequent.

At Aralier *eriwanensis* was sympatric with *V. r. raddei* in a mosaic distribution, where *raddei* was somewhat more connected to the rocks and stones in the habitat and *eriwanensis* more to the grassy spots and junipers growing around. However, large overlap in utilized space was noted in spite of the different ecologi-

cal niche choices. Large orthopterans as probable prey target were abundant everywhere. Nearby *Macrovipera lebetina obtusa* also occurred, at slightly lower altitude, a pattern very similar to what was observed earlier at the Aras valley in the Kars territory, eastern Turkey (NILSON *et al.* 1988).

Taxonomic entity. *Vipera eriwanensis* is a well-defined taxon, not close to any other here-examined sample. However, it has occasionally been treated as a part of a somewhat larger assembly of taxa (as here defined), including the Iranian *ebneri* populations.

Some Turkish *eriwanensis* populations are not clearly understood. The single specimen reported by EISELT (1976) from the Palandöken Mountains, south of the town Erzurum, province Erzurum, in eastern Anatolia, and which is the westernmost locality for this taxon and the only one south of the Arax river, is unique in having two canthalia on each side of head. Midbody scale rows could not be counted as the specimen was mangled. Possible similarities with *anatolica* should be investigated according to the Anatolian dispersal hypothesis (NILSON & ANDRÉN 1987, NILSON *et al.* 1990).

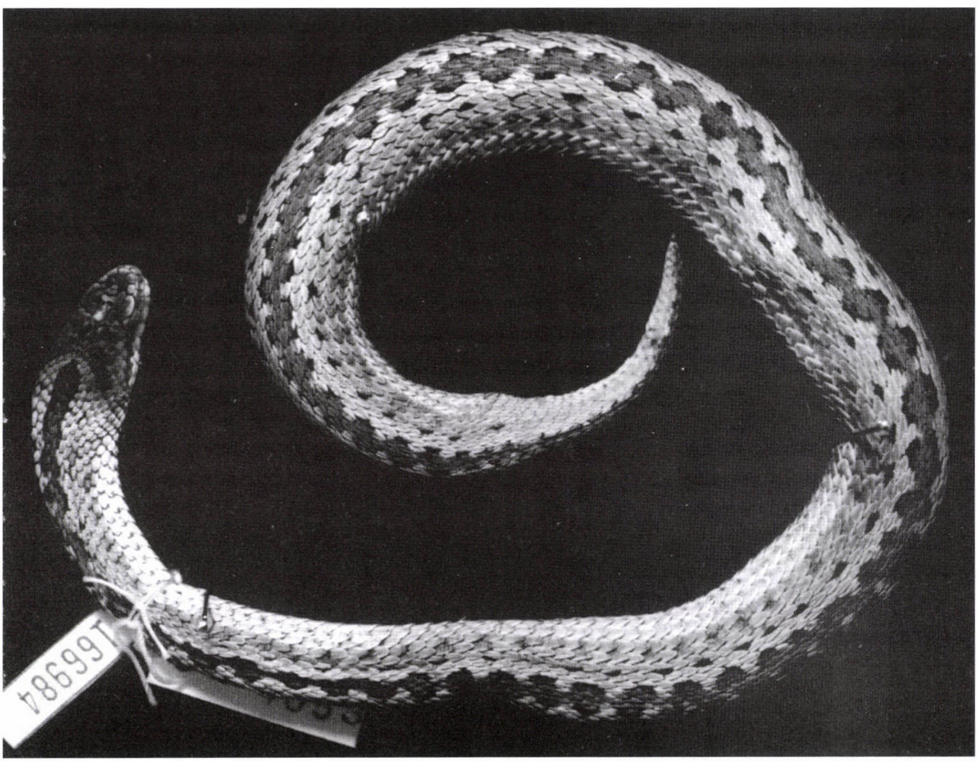


Fig. 58. Female *V. ebneri* (UMMZ 166984) from the Lar valley, Elburz Mountains, Iran

The Kömürlü specimen described by BASOGLU, and which is no. 1 in his series describing *Vipera berus ornata* (BASOGLU 1949), has been referred to *Vipera ursinii renardi* (=*eriwanensis*) by MERTENS (1952*a,b*) as well as by later workers (e.g. KRAMER 1961, BARAN 1976), together with the Sarakamish specimens (nos 2–4 in the Basoglu series). The Sarakamish specimens are clearly *V. u. eriwanensis*, but the single Kömürlü viper is, according to the brief scalation measurements and colour pattern mentioned by BASOGLU, not a typical *ursinii* s. l. at all. We have earlier postulated its belonging to *Vipera pontica* as a possibility (BILLING *et al.* 1990). We were only able to observe *Macrovipera lebetina obtusa* during a visit to Körmürlü in 1988. The lectotype of *V. b. ornata* is a *V. kaznakovi* from Hopa and the name *V. berus ornata* BASOGLU 1947 (non *Mesocoronis ornata* REUSS 1930) is a synonym of *kaznakovi*.

This taxon constitutes of 'population 1' of *Vipera ursinii eriwanensis*, sensu JOGER (1984), and population A of *Vipera ursinii eriwanensis*, sensu BRODMANN (1987).

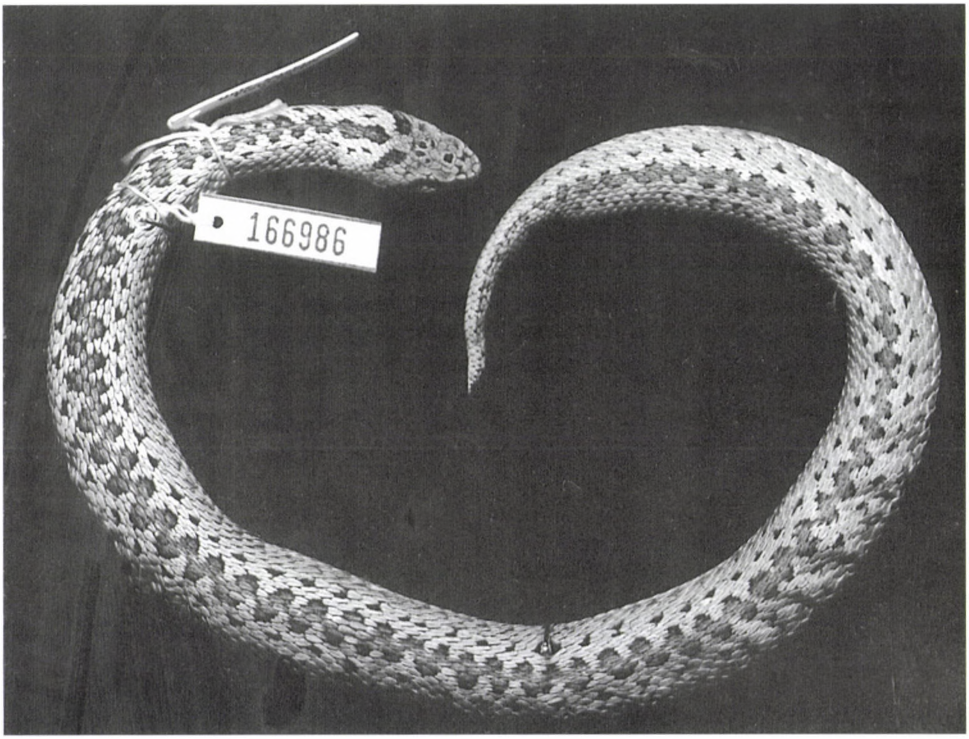


Fig. 59. Female *V. ebneri* (UMMZ 166986) from the Lar valley, Elburz Mountains, Iran

Turkish and Armenian localities and material examined. Turkey: Prov. Kars, Asbua (NHMG 1354.94–95, ZIG 148–150, ZIG-field – 4 sloughs, 2 unregistered specimens); Prov. Kars, E. Kagizman (ZIG-field – 7 unregistered specimens); Prov. Kars, Arpacay (ZIG 262, 3 sloughs – leg. Teynie);

Armenia: rip. Günei, pr. Ardanyc, Gokasse (= Sevan lake) (NHMG 1354.60–61); berg Ara-Iler (NEOTYPE – GNM Re.ex. 5158; ZIG 16 unregistered specimens); lake Sevan area (MTKDD 11160, 20416, 26183); N. Yerevan (MTKDD 17296); Sar (MTKDD 20706); Pambaksky range, Akhundov, 2500 alt (ZISP 17808).

Vipera ebneri Knoeppfler et Sochurek, 1955, **new comb.**
"Iranian mountain steppe viper"
(Figs 58–60)

Vipera ursinii ebneri Knoeppfler et Sochurek, 1955. Burgenl. Heimatbl. 17(4): 185–188. – Terra typica: between Rhema and Demavand, Elburz Mountains, North Iran, 2700 m altitude. Holotype: Naturhistorisches Museum Wien, no. 14889. Leg. R. Ebner, 1936.

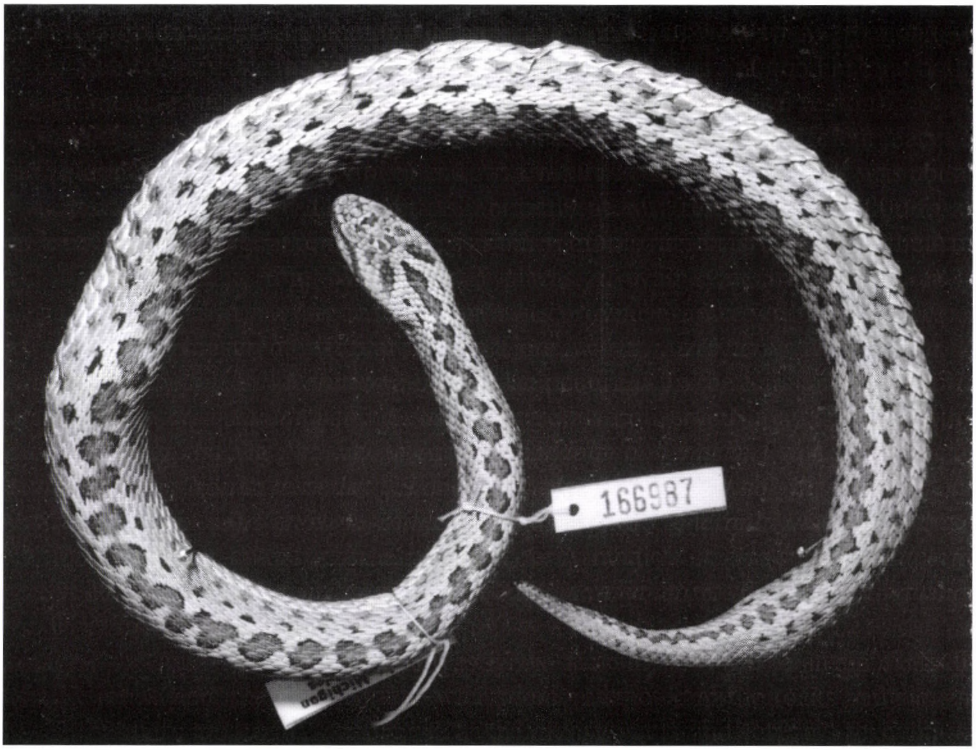


Fig. 60. Female *V. ebneri* (UMMZ 166987) from the Lar valley, Elburz Mountains, Iran

Vipera ursinii renardi, (part). Kramer 1961. Rev. Suisse Zool. 69: 627–722 (member of his "Subalpine Form", a group where he also includes specimens later designated as *Vipera dinniki* and *Vipera darevskii*).

Vipera ursinii eriwanensis (part.), JOGER 1984. Beihefte zum Tübingen Atlas des Vorderen Orients. Reihe A, Nr. 12, 115 pp.

Description. It is a small to medium sized taxon. Maximum total length in our material is 42.8 cm for males (of which tail length is 3.9 cm), and 43.8 cm for females (tail 3.5 cm).

Head pattern present. Lateral body pattern present in most specimens, but weakly developed. Belly-pattern white. Dark labial sutures absent; occipital and postorbital stripes on lateral and dorsal sides of head present; weakly developed bilineate ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings.

Normally nine supralabials on each side (occasionally from eight to ten) and with the fourth under orbit. Three to six loreals on each side. Nasal mostly normal, occasionally with an upper nasal split (in slightly more than 30% of the cases); upper preocular mostly in contact with the nasal; parietals mostly divided (in almost 70% of the cases).

A markedly late reduction of dorsal scale rows (from 21 to 19 rows at an average position approaching the 80th ventral) i.e. 21 dorsal scale rows on neck, anterior part and midbody, and 17 anterior to anal plate. Low number of ventrals, and low number of subcaudals (e.g. compared with *eriwanensis*).

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 16 specimens of both sexes are as follows: preventrals: 1.88±0.16; ventrals: 129.88±0.79; scale rows on neck: 21.00±0.00; scale rows on midbody: 20.75±0.13; posterior scale rows: 17.06±0.06; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 77.19±4.50 and 59.44±3.51 respectively; supralabials (sum of both sides): 18.00±0.13; sublabials (sum of both sides): 20.25±0.30; circumoculars (sum of both sides): 17.69±0.22; loreals (sum of both sides): 7.94±0.36; crown scales (intercanthals and intersupraoculars): 12.06±0.39; dorsal windings/blotches: 60.19±0.89.

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small size
3. Weakly bilineate
4. White belly
5. Lateral blotches and spots present
6. No dark sutures on labials
7. Dorsal zigzag band with rounded corners of windings
8. Medium number of dorsal windings
9. Nasal with an upper nasal split in around one third of the cases
10. A high and narrow rostral
11. A high loreal number
12. Medium number of circumoculars
13. Upper preocular in contact with nasal in most of the cases (more than 60% of the cases)
14. Medium to high number of crown scales

15. Parietals normally fragmented
16. Many supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Many sublabials
20. More mental scales
21. Posterior dorsal scale row reduction, 21 rows on neck and on midbody
22. Low ventral number
23. No exposed intersquamose area.
24. Lower number of subcaudals
25. Alpine/subalpine steppe inhabitant

A taxon in the *Vipera ursinii* complex characterized by an external morphology evolved as typical for mountain taxa of the *ursinii* complex, with small size and whitish belly. It differs from lowland *renardi* and all Asian mountain taxa by having a lower number of ventrals (123–134: X<130), which are whitish in colour; and low subcaudal numbers (23–34: X<31 in males; 19–25: X<24 in females). Labials light and lacking dark sutures. 21 midbody scale rows. Rostral plate higher than wide. It differs further from European mountain populations by having a high number of supralabials.

Both KNOEPFFLER and SOCHUREK (1955) and DELY and STOHL (1989*b*) pointed out the unusual phenomenon of the absence of dark supralabial sutures in the type specimen, a fact that seems to be the situation for all north Iranian and Azerbaijan *ebneri*. The morphological description of *V. u. ebneri* by SAINT GIRONS (1978) and by DELY & STOHL (1989*a, b*) are based on populations here separated as *eriwanensis, ebneri* and *tienshanica*.

Distribution (Fig. 70). *Vipera 'renardi' ebneri* occurs in the Talyish Mountains, Azerbaijan and northern Iranian mountain ranges (Elburz Mountains). The occurrence of '*ursinii*' (=*ebneri*) in Iran was first reported by WETTSTEIN (1952). The main distribution of *ebneri* is known from Central Province (Lar Damavand, Firouz Koh Mountain, Kandovan), Mazanderan Province (Kalardasht, Takhtehsuleiman), Eastern Azarbaijan Province (Tabriz, Mianeh), Western Azarbaijan Province (Tekab) and Zanjhan Province (Zahron, Valaiosh) in Iran (LATIFII 1985, 1991). See also ALIEV and GANIEV (1985) for the distribution in Talyish in Azerbaijan.

Estimated population size. According to LATIFI (1991), the species is widespread in Iran in suitable habitats. The actual distribution is restricted to northern and northwestern Iran.

Habitat. The habitat is given as rural plains, alpine mountains, grasslands, rock-beds (LATIFII 1991). We found the habitat types in the Lar valley, Elburz

Mountains, similar to areas inhabited by the Armenian *eriwanensis*. The habitat can be characterised as alpine steppe (Fig. 61).

Field observations. Several live specimens were observed at the State Razi Serum Institute at Hesarak/Teheran. The habitats were visited in the Lar valley in 1973 and 1976 (ANDRÉN & NILSON 1979) and which consists of several types including high alpine grass steppe. Sympatric, but not always syntopic species in the Lar valley (from where our main series of *ebneri* originates) were *Bufo viridis turanicus, Rana ridibunda, Laudakia caucasia, Lacerta defilippi, Natrix tesselata, Vipera latifii, Agkistrodon intermedius caucasicus.*

Taxonomic entity. Some authors (ENGELMAN *et al.* 1986, SOCHUREK, in litt.) consider *eriwanensis* and *ebneri* as different subspecies while others treat them, together with the populations here denominated as *tienshanica*, as one taxon (*V. u. ebneri* – SAINT GIRONS 1978, 1980, DELY & STOHL 1989*b*, or *V. u. eriwanensis* – JOGER 1984). The "südwestliche Steppenform" of KRAMER (1961) (from Gokcasee, Armenien) is in this paper included in *eriwanensis*. KRAMER (1961) also distinguished a "subalpine form" consisting of a specimen from Elburz, Iran (NMW 14889 = type of *ebneri*) and two specimens of *Vipera berus dinniki*, which he considers synonymous with *renardi*. However, after examining large series of preserved and living specimens of *dinniki* (NILSON *et al.* 1994, 1995) we disagree with KRAMER and follow DAREVSKY (1956, and in litt.) and as JOGER (1984) indicated, by placing *dinniki* as a separate alpine taxon of the *V.kaznakovi* group. ORLOV and coworkers (VEDMEDERJA *et al.* 1986, ORLOV & TUNIYEV 1986, 1990) considered it as a species of its own. Further, one of the three specimens in the "subalpine form" of KRAMER was later included in the type series of *Vipera darevskii* (VEDMEDERJA *et al.* 1986).

Vipera ebneri as here defined constitutes of 'population 2' of *Vipera ursinii eriwanensis*, sensu JOGER (1984), and population B of *Vipera ursinii eriwanensis*, sensu BRODMANN (1987).

Iranian localities and material examined. Iran: Mont Alborz (Elburs), Lar Valley, 2300 m (MHNG 1354.7–10, UMMZ 166983–90, ZISP 17993 – 3 specimens); "Iran" (GNM Re.ex. 680).

Vipera lotievi NILSON, TUNIYEV, ORLOV, HÖGGREN et ANDRÉN, 1995
"Caucasian Meadow viper"
(Figs 62, 63)

Vipera lotievi NILSON, TUNIYEV, ORLOV, HÖGGREN et ANDRÉN, 1995. Asiatic Herpetological Research 6: 1–26. – Terra typica: Armkhi, Checheno-Ingushetia, below Mt. Stolovaya, 2000 m. altitude, Russia (North Caucasus). Leg. K. LOTIEV

Description. It is a small to medium-sized taxon. Maximum total length in our material is 46.8 cm for males (of which tail length is 5.6 cm), and 60.0 cm for females (tail 5.3 cm).

Head pattern and lateral body pattern present in most specimens. Belly-pattern white (in about 80% of the cases). Dark labial sutures lacking or very weakly developed (present in less than 30 % of the cases); occipital stripes of head present; unicoloured bronze or typical "*ursinii*" ground colour; dorsal pattern consists of a zigzag band with rounded corners of windings or pronounced bilineate type of pattern. A certain fraction of the specimens lack pattern (unicoloured bronze).

On average nine supralabials on each side (occasionally from eight to ten) and with the fourth under orbit. Two to six loreals on each side. Nasal normal with an upper nasal split in half of the cases; upper preocular mostly in contact with the nasal; parietals mostly not divided (in around 14% of the cases).

A more posterior reduction of dorsal scale rows (from 21 to 19 rows at an average position near the 87th ventral) i.e. 21 dorsal scale rows from neck to midbody, and 17 anterior to anal plate. (However, there is a great span in the level of reduction: from the 17th to the 106th ventral plate). High number of ventrals, and high number of subcaudals.

In Tables 5 to 36 general and sexual divergence in several phenetic characters are listed, while pooled mean values ± S.E. for 19 specimens of both sexes are as follows: preventrals: 2.37±0.11;

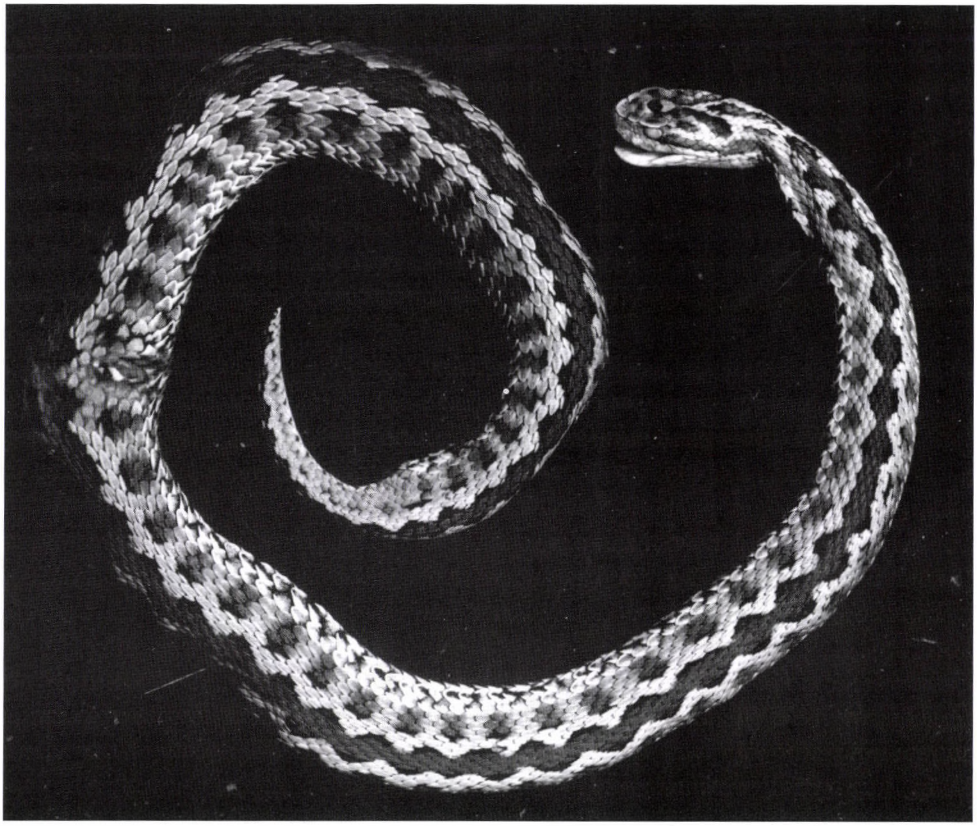


Fig. 62. Female holotype of *V. lotievi* (ZISP 20305), Itum-Kali, Checheno-Ingushetia, north Caucasus

ventrals: 140.95±0.56; scale rows on neck: 21.00±0.00; scale rows on midbody: 20.89±0.14; posterior scale rows: 17.00±0.00; level of scale row reduction from 21 to 19 rows (at ventral number, and in%): 92.92±3.87 and 65.85±2.71 respectively; supralabials (sum of both sides): 17.21±0.20; sublabials (sum of both sides): 20.21±0.41; circumoculars (sum of both sides): 18.11±0.44; loreals (sum of both sides): 8.05±0.46; crown scales (intercanthals and intersupraoculars): 10.11±0.64; dorsal windings/blotches: 64.86±2.22.

A taxon of the *Vipera ursinii* complex characterized by a unique molecular profile. It is similar to the pattern of *renardi* and *eriwanensis*, but separated from both by unique fixed loci as indicated by electrophoretic studies of isoenzyme (NILSON *et al.* 1994, 1995).

Diagnosis. A species within the *ursinii* complex that differs from all other taxa in the complex by the combination of having:

1. Small to median size
3. Typical pattern, 'bilineate' pattern, or unicoloured
4. White belly
5. Lateral blotches and spots present or absent
6. Normally no dark sutures on labials
7. Dorsal zigzag band with rounded corners of windings, strongly bilineate, or unicoloured bronze
8. High number of dorsal windings (when present)
9. Upper nasal split present or absent (in equal proportions)
10. A somewhat high and narrow rostral
11. A medium loreal number
12. Medium number of circumoculars
13. Upper preocular in contact with nasal
14. Not many crown scales
15. Parietals normally not fragmented
16. Few or variable number of supralabials
17. Posterior supralabials not very much smaller than anterior ones
18. Fourth supralabial below orbit
19. Many sublabials
20. Medium to low number of mental scales
21. Posterior neck dorsal scale row reduction, 21 rows on neck and midbody
22. High ventral number
23. No exposed intersquamose area
24. High number of subcaudals
25. Alpine/subalpine steppe inhabitant

A species of the *Vipera ursinii* complex characterized by polymorphism in colour-pattern, including "bilineate pattern" of the same kind as in some *V. seoanei*, and "bronze" unimorphs, similar to some *V.dinniki*. External morphology evolved as typical for mountain taxa of the *ursinii* complex but distinct from all other mountain taxon in colour pattern.

From the allopatric *renardi*, it differs besides colour pattern in morphology by having light supralabials (sutures heavily striped in black in *renardi*), a higher rostral index, smaller size, white belly (dark in *renardi*), and a different niche by being alpine (*renardi* is a lowland steppe inhabitant). No future reproductive cohesion can be postulated.

It is separated from the likewise allopatric *eriwanensis* in the Armenian highlands by the semidesert lowland Kura river valley that separates the Large Caucasus from the Small Caucasus. No connection can be postulated in an evolutionary time frame. Besides colour pattern there is a differentiation in morphology as *eriwanensis* has a higher number of crown scales and a somewhat lower ventral count, and preocular separated from nasal to a higher extent.

Besides the variation in scalation, a pronounced variation in colour and pattern is expressed. Most striking, and unique for the entire *ursinii* complex, is the bronze morph, which is found in 25% of the investigated specimens (N=40).

From the sympatric *Vipera dinniki* it differs in several scalation characters and in the colour of the belly. In *lotievi*, the belly is generally white, preocular in contact with nasal, snout concave, 138 or more ventrals, always a single apical, less fragmented crown scales (7–16), parietal ocellated spot present, iris not gold-edged in life. In *V. dinniki* the belly is black, preocular separated from nasal, snout not concave, 136 or less ventrals, apical single or divided, more fragmented crown scales (10–21), no parietal ocellated spot, iris gold-edged in life.

Distribution (Fig. 70). The populations of the *V. ursinii* complex from the Great Caucasus, which are generally referred to *renardi* in literature, belong to this taxon. The distribution of *renardi* in published maps (e.g. BANNIKOV *et al.* 1977) from these mountains must be referred to *lotievi* in most cases. However, the extremely polymorphic *Vipera dinniki* is partly sympatric with *lotievi* in the Caucasus. The former expresses morphs with great similarity with *'ursinii'* in colour and pattern (NILSON *et al.* 1995), and the two taxa where frequently confused in former days (e.g. KRAMER 1961). Several of the dots on the distribution maps of *'renardi'* from the Caucasus in JOGER (1984) and BANNIKOV *et al.* (1977) must be referred to *'ursinii'* similar morphs of *V. dinniki*. *Vipera lotievi* is distributed in the semiarid 'hollows' between the northern slope of the main Caucasian range and Skalisty range from upper part of the river Kyafar (range Abishir–Akhuba) eastward to inside Daghestan. Altitudinal span in this region goes from 1200 m up to 1800m, but occasionally up to 2700 m. Further, it is registered from Mt. Elbrus in the Central Caucasus, and mountains north of Lagodechi in the eastern Caucasus, besides several isolated records from the eastern and Central Caucasus range. Recently (1995) it was discovered in the Western Caucasus (Laba river region) in dry mountain meadows within the range of *Vipera dinniki* (TUNIYEV, pers. comm.), and not far from the type locality of the latter.

Habitats. Typical habitats are oreoxerophytic landscapes with semiarid light-forests (like Shibliak), phrygana (with 'tragakant' *Astragalus*), which are very similar to east-Mediterranean types of vegetation. On the upper elevation of the distribution, *V. lotievi* reaches the subalpine mountain belt.

Taxonomic entity. *Vipera lotievi* is a well-defined taxon, not close to any other here-examined sample. However, it has occasionally been treated as a part of *Vipera renardi*, and occasionally *Vipera dinniki*. Results from a separate study of these alpine Caucasian populations of the *Vipera ursinii* complex is published elsewhere (NILSON *et al.* 1994, 1995).

Russian, Georgian and Azerbaijan localities and material examined. Russia: holotype: ZISP 20309, Armkhi, Checheno-Ingushetia, below Mt. Stolovaya, 2000 m. altitude; Paratypes; ZISP 20305, Itum-Kali, Checheno-Ingushetia; ZISP 20310, Armkhi, Checheno-Ingushetia, below Mt. Stolovaya, 2000 altitud; ZISP 20304, vicinity of village Armkhi, Checheno-Ingushetia; ZIG 298–306, river Chanty-Argun w. Itum-Kali, Checheno-Ingushetia; ZISP 20307, Itum-Kali, Checheno-Ingushetia; ZISP 20312, Armkhi, Checheno-Ingushetia; ZISP 20313, Armkhi and Mt. Stolovaya, Checheno-Ingushetia; Checheno-Ingushetiya, Armchi town, N. Caucasus (ZIG 4 unregistered live specimens); ZIG 297, Mt. Elbrus; ZISP 18203, Teberda, State reserve, Mt. Bolshaya Hatipara; ZISP 18226, Kabardino-Balkaria, vicinity of village Terskol; ZISP 11996, Caucasus, Gunib, Dagestan;

Georgia/Azerbaijan/Russia (Dagestan) border area: ZISP 20303, Lagodechi.

SUPPOSEDLY RELATED TAXA WITH AFFINITY NOT FINALLY SOLVED

Vipera darevskii VEDMEDERJA, ORLOV et TUNIYEV, 1986
"Darevsky's viper"
(Fig. 64)

Vipera kaznakowi dinniki DAREVSKY, 1956, Bulletin of the Academy of Sciences of Armenia, Yerevan 9(12): 127–130.

Vipera ursinii renardi, (part). Kramer 1961. Rev. Suisse Zool. 69: 627–722 (member of his "Subalpine Form", a group where he also includes *Vipera dinniki* and *Vipera renardi ebneri*).

Vipera kaznakowi darevskii, VEDMEDERJA 1984, *nomen nudum*. *In:* Species and its Productivity in the Habitat. Part V. Questions in Herpetology, Sverdlovsk 8: 8–9. [in Russian]

Vipera darevskii, VEDMEDERJA, ORLOV & TUNIYEV 1986, Proc. Zool. Inst., Leningrad 157: 55–61. – Terra typica: Mt. Legli, Dzhavakhetsky Ridge (Mokrye Mountains), northwestern Armenia. Holotype: ZISP 19934. Coll. DAREVSKY 1980.

Distribution. The known range of this taxon is restricted to Mt. Legli, the southeastern part of the Dzhavakhetsky Ridge (Mokrye Mountains), northwestern Armenia (Fig. 70).

Comments. External morphology evolved as typical for many alpine taxa within the *ursinii* complex, but shows clear similarities also with members of the *Vipera kaznakovi* group (Orlov and Tuniyev, 1990). The phylogenetic position for this taxon is not yet clearly reconstructed, and despite its strong affiliation to the *kaznakovi* group, it shows some intermediate characteristics, and is therefore here included in this overall review.

One of the three specimens of *Vipera ursinii renardi* in the "subalpine form" of KRAMER (1961) was later included in the type series of *Vipera darevskii* (VEDMEDERJA *et al.* 1986). Research is going on for a genetic analysis (in prep.).

Field observations. We observed ten specimens of *Vipera darevskii* in Northwestern Armenia at Mt. Legli in 1993. The habitat, normally at between 2600 and 3000 m altitude, can be characterised as alpine short, grazed meadows in a hilly surrounding, and with piles of flat stones. Sympatric and syntopic with *Coronella a. austriaca* and *Lacerta valentinii*.

Vipera pontica BILLING, NILSON et SATTLER, 1990
"Pontic viper"
(Fig. 65)

Vipera pontica, BILLING, NILSON et SATTLER, 1990, Zool. Scripta 19: 227–231. (Figs 1–4) – Terra typica: Coruh valley, prov. Artvin, northeastern Turkey. Holotype: Göteborg Natural History Museum, Re.ex. 5021. Leg: Sattler 1989.

Distribution. The known range of this taxon is restricted to the Coruh valley, Artvin province, northeastern Turkey. It may also occure in the Erzurum province, Turkey, and in the Kura valley, Georgia. Recently BARAN and ATATÜR (1998) reported a specimen from Camlihemsin, province Rize, Turkey.

Comments. Considered to be of uncertain relationship, and tentatively included in the *ursinii* complex by MCDIARMID *et al.* (1999, p. 412), but no new indications for this statement are given. We consider it to be well outside the *ursinii* complex, but it certainly needs additional studies. The taxon is not further discussed in this work.

KEY TO THE VIPERA URSINII COMPLEX

The taxa within the *ursinii* complex are difficult to key out because of homoplasies due to morphological convergences and parallel adaptations to similar environments. The key is merely a help to determine problematic specimens, but considerable care must be taken all the time. Meanwhile, other species can also show great similarity in characters with the members of the *ursinii* complex, like *Vipera berus* (to *renardi*) and *Vipera dinniki* (to *lotievi*).

Members of the *ursinii* complex (*Acridophaga*) generally have a single apical shield in contact with rostral. Almost all members of the subgenus *Pelias* are characterised by having two apicals in contact with rostral, except *dinniki, darevskii* and *kaznakovi*, which are variable in this character.

The *ursinii* complex is sympatric with *Vipera dinniki* (through *lotievi*) in the Great Caucasus. However, *Vipera dinniki* has the preocular separated from the nasal, black belly, higher fragmentation of crown scales (mean number more than 12), lower number of ventrals (mean less than 136) and lacks a frontal/parietal ocellated spot, which is characteristic for members of the *ursinii* complex. Further, in *dinniki* (like *kaznakovi*) the iris is gold-edged in life. In addition, *V. lotievi* has a more concave snout with pronounced canthus rostralis.

Vipera kaznakovi is allopatric with *V. eriwanensis* while *Vipera darevski* is parapatric. In the key, *Vipera darevski* will fall out as *eriwanensis*.

Melanism is the normal adult colour pattern in *Vipera nikolski* and mostly so in *V. barani*. It also is frequent *V. berus, V. bosniensis, V. dinniki* and *V. kaznakovi*. It is absent in the *ursinii* complex (dorsal partial melanism can occasionally be seen; e.g. *macrops*), except in a few populations of *renardi* north of the Great Caucasus.

1a Dorsal windings 34–42 (X=38); ventrals 114–124; high loreal number (6–12, X=9.5*); rostral index mean (height/width) 1.27; 19 midbody scale rows; at high altitude in West Turkish Anatolia *anatolica*

1b Dorsal windings more than 45(41); ventrals much more than 120 (in nearly every case); high to low loreal numbers; rostral index mean (height/width) less than 1.24 (in most cases close to 1); 19 or 21 midbody scale rows. Not in West or Central Turkish Anatolia 2

2a 19 dorsal scale rows on middle of body (single specimens with 21 rows in all taxa, except *ursinii* and *graeca*) 3

2b Twenty-one dorsal scale rows on middle of body (single specimens in all taxa, except *eriwanensis*, with less than 21 rows) 8

3a Nine supralabials; upper edge of the nasal plate not notched; more than four loreals on each side; dorsal side of head concave; high altitude; Xinkiang, China *parursinii*

3b Eight or less supralabials; notched upper and posterior edges of the nasal plate; four or (more often) less loreals on each side; plain dorsal side of head 4

4a Reduction from 21 to 19 scale rows on anterior part of body, normally posterior to the 7th ventralia; exposed black intersquamose area of around one third scale-width; frontal and parietals normally unfragmented; increased size; comparatively short tail; normally 4 or 5 scales in mental row; higher number of ventrals (from 130 to 145 in 94% of the snakes); clear bilineate lateral and dorsal ground colour; belly colour blackish with white spots; broad postocular band that covers most of third temporalia; lowland inhabitant 5

4b Reduction from 21 to 19 scale rows on neck, normally anterior to the 8th ventralia; no exposed intersquamose area; frontal meanwhile and parietals more often fragmented or divided; reduced size; comparatively long tail; normally 3 scales in mental row; reduced number of ventrals (from 120 to 135 in 98% of the snakes); no pronounced bilineate lateral and dorsal ground colour; belly colour mostly whitish with black spots; narrow or reduced postorbital band that covers less than half of the third temporalia; alpine 6

5a Mean around 132 ventrals; undivided frontal; dark labial sutures missing; number of zigzag windings slightly less (X=53); loreals between 2–9* (X=5.5); mean number of circumoculars around 17*; frontal spot without light border *rakosiensis*

5b Mean around 138 ventrals; divided frontal in 20% of cases; dark labial sutures resent; number of zigzag windings slightly more (X=57); loreals between 4–15* (X=8.6); mean number of circumoculars around 19*; frontal spot ocellated *moldavica*

6a Always 17 dorsal scale rows on posterior part of body; normally 8 supralabialia on each side; fourth supralabialia under eye; posterior supralabials only less small than anterior; frontal undivided; Central Italy, Southeast France *ursinii*

6b Occasionally fewer than 17 dorsal scale rows on posterior part of body; normally 7 or 6 supralabialia on each side; a tendency to having third supralabialia under eye; posterior supralabials markedly smaller than anterior; frontal often somewhat fragmented 7

7a Seven or fewer sublabials on each side; less than 25 subcaudals in males, less than 20 in females; nasal plate often divided, fragmented or united with prenasal; lateral body blotches missing or very week (in males); no dark labial sutures; Greece *graeca*

7b More than seven sublabials on each side; more than 25 subcaudals in males, more than 20 in females; nasal plate normally undivided; lateral body blotches present; dark labial sutures; Kroatia, Bosnia, Herzegovina, 'Yugoslavia, Albania *macrops*

8a Supralabials and throat marked blackish; dark ventral side; belly black or blackish with light dots; large adult size (>44 cm); lateral body pattern of larger blotches; 135–150 ventrals; lowland and foothill steppe habitats; S. Russia, N.Azerbaijan, Ukraine, Kazakhstan *renardi*

8b Supralabials and throat whitish; white ventral side; small adult size (<44 cm); lateral body pattern of narrow stripes; 123–151 ventrals; from hilly steppe to alpine steppe and meadow habitats 9

9a Low ventral numbers (123–134: X<130); low subcaudal numbers (23–34: X<31 in males; 19–25: X<24 in females); light unicoloured labials; Iran, Azerbaijan *ebneri*

9b Higher ventral numbers (129–145: X>135); high subcaudal numbers (30–39: X>35 in males; 23–30: X>25 in females); labials with somewhat dark sutures 10

10a Preocular(s) often separated from nasal (in about 77% of the snakes); frontal individed; posterior scale row reduction (mean at ventral 95); infrequently two apicals (in 27% of the snakes); Armenia, Azerbaijan, east Turkish Anatolia *eriwanensis*

10b Preocular(s) in contact with nasal; frontal more often divided (up to 33% of the snakes); midbody scale row reduction (between ventrals 17 and 106; mean from ventral 88 or earlier); normally a single apical 11

11a Less fragmented upper head plates (parietals and frontal divided in 14.3% of the snakes; 7–16 intercanthals and intersupraoculars); normally with nasal split (in more than half of the specimens); polymorph in colour pattern (classic pattern of "*seoanei*-" and "*dinniki*-type", or uniform (="bronze-type")); when zigzag pattern present, a higher number of windings (50–81: X=65.5); Great Caucasus (Russia, Georgia, Azerbaijan) *lotievi*

11b More fragmented upper head plates (parietals generally divided and frontal divided in half of the snakes; 8–22 (intercanthals and intersupraoculars); normally without nasal split (only in one tenth of the specimens) 12

12a Dorsal pattern of typical "*ursinii*-type" with a lower number of zigzag windings (41–58: X=48.2); S. Kazakhstan, Kirgizia, Uzbekistan, Tadjikistan, West Xinkiang (China) *tienshanica*

12b Dorsal body pattern of series of transverse bands or angled zigzag band (64–71 zigzag turns or transverse bands); supralabial sutures weekly blackish in males only; E. Kazakhstan (Altai Mountains, Saur Mountains), NW China (Altai) the 'Altai form of *renardi*'

*=sum of left and right side

The Asian taxa within the complex can be difficult to key out, and the following can be to some help:

1. *Renardi* is strongly built and broad-set, with black belly. The dorsal pattern consists of black-edged rhombic or round spots, which are sidewise displaced and thereby forming a dorsal wavy zigzag band.

2. *Tienshanica* is a shorter snake (like *anatolica*), with whitish belly. The smaller size is reflected by the rather few ventrals, and the low number of dorsal windings in the zigzag band. The latter varies much, from smoothly rhombic zigzag (*renardi* kind) to sharp angle-edged zigzag (the 'Altai form of *renardi*' kind). The dorsal spots are black-edged. It has fewer circumoculars than in *parursinii*.

3. *Parursinii* is also a short snake with whitish belly. The dorsal pattern consists of black-edged round or rhombic spots, which are sidewise displaced to form a zigzag band (of the *renardi* kind). Being unique by having only 19 neck and midbody dorsalscale rows.

4. The 'Altai form of *renardi*' is also a small snake with whitish belly. However, it has a very high number of ventrals, and dorsal windings in the zigzag band. The latter normally consists of transverse bands or sharply angle-edged zigzag windings. The dorsal pattern is normally not black-edged, nor rhombic (less than 10% has a '*renardi*-pattern').

DISCUSSION

Relationships within ursinii *s. l.*

1. Immunological and electrophoretic studies (JOGER *et al.* 1992, NILSON *et al.* 1993, NILSON *et al.* 1994) analysed with cladistic phylogenetics support a north-south relationship.

2. As demonstrated in this paper several morphological character states used in earlier phylogenetic discussions are reversals and convergence (e.g. 19 midbody scale rows).

3. A cladistic analysis of the re-evaluated morphological information (2) results in a phylogenetic reconstruction, which in its major lineages is concordant with the molecular analysis (1).

Therefore we believe in a north-south directed phylogenetic pattern and reject a west-east alternative. Phylogenies are hypotheses, but in this case we consider our phylogeny as a more appropriate alternative as it is based on cladistic phylogenetics, and supported by two alternative approaches: molecular and morphometric. The division of *Vipera ursinii* into four subspecies by KRAMER (1961), SAINT GIRONS (1978) and BARON (1992) is a phenetic approach. In their model *renardi* is distributed in lowland CIS and *rakosiensis* in the Hungarian puszta respectively, and with *ebneri* occurring from the Armenian plateau to China, and *ursinii* from France to West Turkey. That taxonomy is also repeated in GOLAY *et al.* (1993) with the name *ebneri* replaced by *eriwanensis*. This nomenclatorical framework does not reflect the historical evolution of the group, and hence gives a taxonomy that does not reflect the phylogeny. All these subspecies (sensu SAINT GIRONS) except *rakosiensis* are in fact polyphyletic.

Species concepts are focusing on interbreeding or on common descent. We are advocates of a concept where taxa are terminal ends of evolutionary lineages (CRACRAFT 1989, FROST & HILLIS 1990, CROTHIER *et al.* 1992, etc), and we can not follow the subspecific division stated above. Thus, the systematic pattern for *Vipera ursinii* s. l. is rather complicated. We feel that our results would justify a quite different taxonomic pattern that would better reflect the evolutionary history.

The electrophoretic serum protein patterns are population specific for the compared samples except for the French and Italian *ursinii* (=*ursinii* and *wettsteini*, sensu KNOEPPFLER & SOCHUREK (1955)), which are not well distinguished from each other (Fig. 67). The difference between these two populations (based on specimens from Mt. de Lure and Sibillini respectively) is not bigger than between specimens of each sex from the latter locality (JOGER *et al.* 1992). As stated before (JOGER *et al.* 1992, NILSON *et al.* 1993), *anatolica, graeca*, French and Italian *ursinii*, and *moldavica* differ from each other and from all others in their main an-

odic bands. And this to a degree that is usual only seen on species level. Albeit a small sample, no intra-population polymorphism could be demonstrated in these anodic bands, except when comparing *renardi* from the western steppes (Ukraine) and from the eastern ones (Kazakhstan). Thus eight different operational taxonomic units (OTUs) are distinguished (nine if the two lowland *renardi* groups are included as different groups; a fact that is in line with the demonstrated morphological differences between the latter two).

The analysis of immunological distance between the albumins (JOGER *et al.* 1992) of these OTUs resulted in three groups of taxa (clades – Fitch-Margoliash, Wagner trees; "phenetic" clustering (UPGMA, Fig. 66)):

1. a Balkan clade with *graeca, macrops* and *moldavica*;
2. a Central European clade with *rakosiensis* and *ursinii*; and
3. an eastern clade including *renardi, eriwanensis* and *anatolica*.

The latter two clades separate from the Balkan one by a distance equivalent to that between full species (at least seven distance units). As a comparison, this is equal to the distance between *Vipera ammodytes* and *Vipera latastei* (HERRMANN *et al.* 1992). Furthermore, similar distances separate *moldavica* from *graeca–macrops*, and *anatolica* from *renardi–eriwanensis*. On the other hand, *rakosiensis* cannot be significantly separated from *ursinii* with this method. Thereby the immuno-

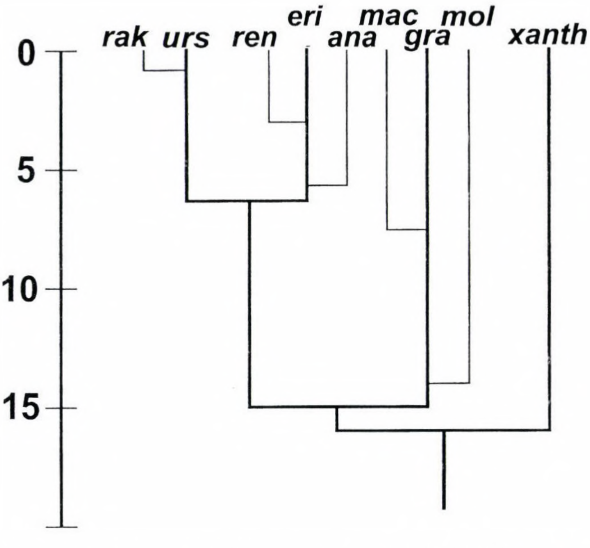


Fig. 66. The UPGMA tree for reciprocal distances (heavy lines), (F=3.02), supplemented by unidirectional distances (thin lines), (F=15.7). Scale indicates immunological distance corresponding to the respective branching point. *V. xanthina* as outgroup. Redrawn from JOGER *et al.* (1992) (*rak=rakosiensis, urs=ursinii, ren=renardi, eri=eriwanensis, ana=anatolica, mac=macrops, gra=graeca, mol=moldavica, xanth=V. xanthina*)

logical distances indicate a long-time genetic separation between five groups of the taxa investigated:

1. *anatolica*
2. *renardi* and *eriwanensis*
3. French and Italian *ursinii*, and possibly *rakosiensis*
4. *graeca, macrops*
5. *moldavica*,

and which might be regarded as separated species.

Further biochemical investigations of the taxa concerned (NILSON *et al.* 1994) show a possible genetic separation between, on one side, *renardi* (Ukraine, Dnepr) and on the other, *eriwanensis* (Turkey) and *lotievi* (Checheno-Ingushetia). This supports the hypothesis that lowland *renardi* is separated from the alpine Caucasian and Transcaucasian taxa at species level.

This pattern of south-north (alpine-lowland) relations is further supported by the cladistic analyses based on morphology (Fig. 15).

Other taxonomies and phylogenetic explanations, based on the traditional phenetic approach and with a different conclusion than the one expressed earlier (see above), were presented by MÉHELY (1911), and in a slightly modified way by DELY and STOHL (1984, 1989*a*). The latter authors consider *macrops* as a unique taxon well-separated from the Italian *ursinii* and the Hungarian *rakosiensis*. Their analyses were based on scalation morphology, head shape and osteological characteristics. Further DELY and STOHL (1989) stressed that *macrops* is more closely related to the lowland *rakosiensis* than to Western European *ursinii*, and that *ebneri* is more closely related to the northern lowland *renardi*. These conclusions are in agreement with ours except that in our model *rakosiensis* is replaced by *moldavica*. However, *moldavica* is similar to *rakosiensis* in morphology.

Phenetically there are similarities between populations occurring in similar habitats as is discussed in the 'Phenetic analysis, but these must be considered as a homoplasies, and with little phylogenetic information value. Instead, the cladistic analyses of morphology and genetic metabolites pointing in a 'north-south' direction must be preferred.

Paleogeography and the biological clock

Time estimation of two IDUs (Immunological Distance Units) is corresponding to a period of 1 million years in *Vipera* (HERRMANN *et al.* 1992). If the number of IDUs received in the immunological study of different *ursinii s. l.* populations is accurate (JOGER *et al.* 1992), a time branching schedule should be reconstructed (Fig. 68).

The evolutionary history of the *Vipera ursinii* s. l. complex (=*Acridophaga*) is a Neogene event. The complex was separated from the main viper stem about ten million years ago. At that time, a hypothetical ancestral *ursinii* was spread over the Pannonian – Pontian steppes north of the Eastern Paratethys. The Late Miocene consolidated the continental conditions in the Middle East (STEININGER & RÖGL 1984) with a dry steppe like habitat (Pontian–Messinian). A first division of "*ursinoides*" took place during the upper Miocene, somewhere around seven to six million years ago (Fig. 68). During this period, the lowland *moldavica* branched off from the main "*ursinoides*" stem. This branch was somewhat later (around six to seven million y.b.p.) divided into the two branches that led to the present *moldavica* and the *macrops–graeca* group respectively. It is possible that the members of these two branches stayed in lowland habitats for a considerable time.

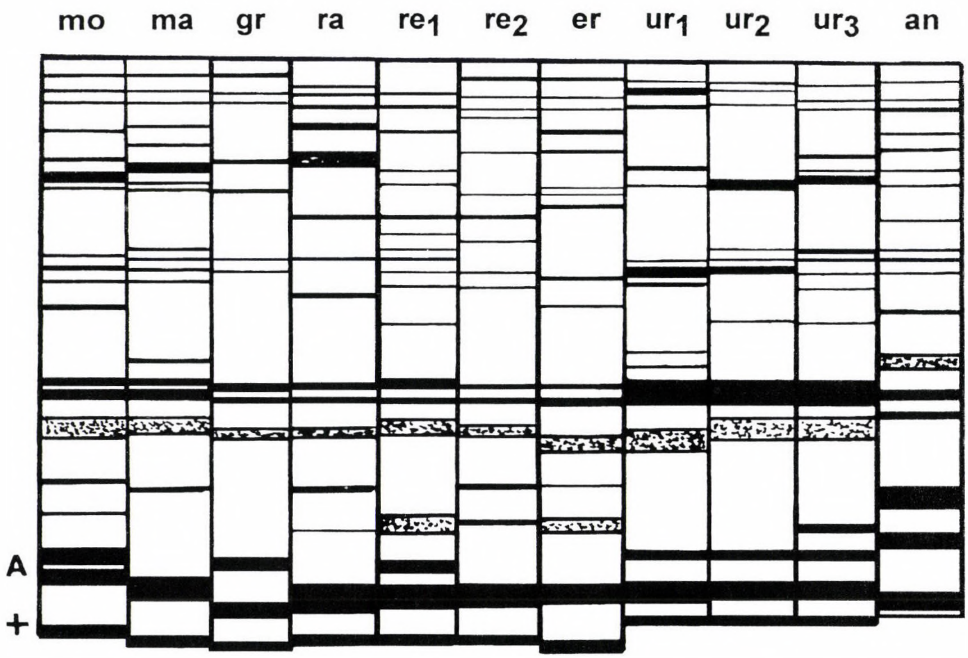


Fig. 67. Electrophoretic patterns of serum proteins of different taxa and populations of the *ursinii* complex. A= main albumin band (mo=*moldavica* (Valea lui David, Roumania); ma=*macrops* (Korita, Bosnia-Herzegovina); gr=*graeca* (Pindos, Greece); ra=*rakosiensis* (Hungary); re1=west-*renardi* (Ukraine); re2=east-*renardi* (Kazakhstan); er=*eriwanensis* (Asbua, Sarakamish, Turkey); ur1=*ursinii*, male (Abruzzi, Italy); ur2=*ursinii*, female (Abruzzi, Italy); ur3 (we)=*ursinii* (Mt. de Lure, France – *'wettsteini'*); an=*anatolica* (Ciglikara, Turkey). Redrawn from JOGER *et al.* (1992)

The *moldavica* branch is still an inhabitant of lowland meadows (with perhaps a few exceptions such as at Mt. Rarau in Romania, and at Sumen and Sofia in Bulgaria).

The distribution of the lowland forms must have been north of the Paratethys Sea and before the Messinian salinity crisis. The Paratethys Sea extended from the Aral Sea area in the east to the Pannonian plains in the west during Miocene (HSÜ & GIOVANOLI 1979, CITA 1982, STEININGER *et al.* 1985). The evaporation of the Mediterranean Sea that took place about 6 million years ago had a strong influence on Paratethys. The Mediterranean Basin was drained and the Paratethys was reduced into a network of lakes that enabled the lowland '*ursinii*' to spread south through a number of passages (e.g. between the Caspian and Black Seas, between the latter and the Carpathian lakes, in between and around the Carpathian lake system etc). The remnant sea systems that characterised Southeast Europe and West Asia during late Miocene made isolation possible in a number of geographical pockets. The splitting of the '*moldavian* group' from the main lineage took place during this period.

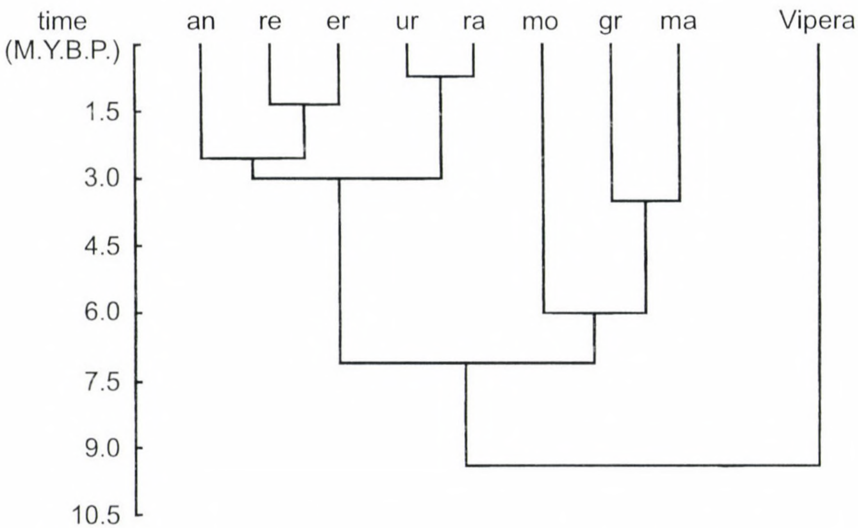


Fig. 68. The approximate branching pattern and the geological time scale (M.Y.B.P.=million years before present) in the *ursinii* complex, based on immunological studies of albumins, and the estimation that two IDUs (Immunological Distance Units) are equal to a time scale of one million years (HERRMANN *et al.* 1992). *ana=anatolica; ren=renardi; eri=eriwanensis; urs=ursinii; rak=rakosiensis; mol=moldavica; gra=graeca; mac=macrops.* The main *Vipera* lineage is represented by *V. xanthina*. Constructed from data in JOGER *et al.* (1992), HERRMANN *et al.* (1992*a*), NILSON *et al.* (1993)

Of the two taxa in the sister group *macrops* is a mountain dweller, but retaining several characteristics of "lowland *ursinii*", such as large size, darker belly etc. The island Krk in the Adriatic Sea is reported to have *macrops*, and this is of course a lowland habitat at sea level. The Greek taxon, *graeca*, seems to be an extreme subalpine inhabitant, and the separation between *macrops* and *graeca* took place in the middle Pliocene, between four and three million y.b.p. This division was preceded by the subdivision of the Eastern Paratethys into smaller basins during the Messinian event. It could have played an important role in the Pliocene fragmentation of the early *macrops*. The origin of these two mountain taxa also coincided with another important event, the Pliocene rise of the alpine mountain chains that subdivided Europe and adjacent West Asia into ecologically different zones.

Thus, each of the three taxa in this *moldavica* lineage shows a long individual evolutionary history.

Contemporary with the division of the East European mountain taxa, i.e. after the salinity crisis and during the rise of the alpine mountain chains, the lowland *rakosiensis* and *renardi* lineages appeared on the scene. The formation of the Carpathian Mountains could have had an effect on this event. Soon afterwards, *anatolica* was split off from the *renardi* lineage. At this time, when the modern Mediterranean Sea was formed, Turkey, Armenia and Iran were separated from the remaining northern and more western parts of the "*ursinii*" range by the flooding that created the Mediterranean. This flooding progressed across the Caucasian foredeep into the Caspian Sea depression and perhaps as far as lake Baikal (STEININGER & RÖGL 1984). This flooding may also have had an affect on the evolution of the 'Altai form of *renardi*', *tienshanica* and *parursinii*.

However, the splitting of *eriwanensis* from the *renardi* lineage took place in the early Pleistocene, about one and a half million y.b.p., which was well after the Pliocene flooding across the Caucasian foredeep. This indicates that the Western and Central Asian populations must have reached this area in at least two waves. The branch that gave rise to *anatolica* was separated from the *renardi* lineage before the Pliocene flooding. Perhaps also *ebneri*, which today is distributed south of the Araxes valley, was separated during this period. However, we do not know the age of this taxon.

The European alpine populations in Italy and France must have split off from the *rakosiensis* stem during the glacial and interglacial periods of middle Pleistocene, roughly about 750.000 years ago. This was certainly also the period when all or most of the local Italian and French populations became isolated from each other. This phenomenon is expressed in the locally very pronounced morphological distinction (e.g. BARON *et al.* 1993).

The fossil record – "ursinii" sensu lato

According to Zerova, there have been no records of fossil *Vipera ursinii* s. l. in the CIS. This depends on the poor fossilisation of the small and delicate skeletons of species like *ursinii* (ZEROVA, in litt.). However, fossil material of small species of *Vipera* (*Pelias*) from Miocene, Pliocene and Pleistocene has been found at the northern coast area of the Black Sea. This is an area that nowadays is inhabited by *Vipera renardi* alone (ZEROVA *et al.* 1986, NILSON & ANDRÉN 1997).

Vipera 'ursinii' rakosiensis has had its twentieth century distribution in the Danube lowland plains (Fig. 69) consisting of the puszta habitats of the great Carpathian Basin that covers part of Austria and Romania, and the whole of Hungary. This Pannonian Basin defined as one of the Mediterranean backarc basins has its origin in the extension and subsidence within the orogenic belt of the Mediterranean-Alpine region (HORVATH & BERCKHEMER 1982). It is bordered by high mountain chains to the west (the Eastern Alps), to the east, southeast and north (the Western, Southern and Eastern Carpathians) and to the South (the mountain plateau of former Yugoslavia, the Dinarides) since before Miocene (AGER 1980). During late Miocene (Messinian-Late Pontian stages) parts of this basin was submerged.

There are quaternary records from further north (SZYNDLAR 1984), where the species occurred as far north as Poland. North of the Vienna basin and along the river Oder there is a lowland connection with the Polish areas where fossil remains of *ursinii* s. l. has been found. A somewhat doubtful record from Czechoslovakia from the beginning of this century (cited in SZYNDLAR 1984) could indicate a connection even in our times if this record is accurate. Otherwise, the actual connection between *rakosiensis* and *renardi* does not go towards east through the Carpathian Mountains as often indicated (the supposed intermediate populations in Moldavia just east of the mountains in Romania (=*moldavica*). The taxon *moldavica* has a southern connection through the lowlands along the river Danube into northeast Bulgaria (Sumen) and further south towards the *macrops* and *graeca* ranges. The specimens found in northwest and northeast Bulgaria, in the area of Sofia and in Sumen, respectively, seem to be *rakosiensis* (BESKOV 1973) or *moldavica*. They were found in typical lowland habitats, even if the two Sofia localities (which are the southernmost of all lowland populations) are situated at 650 and 950 m altitude respectively (as is the Mt. Rarau record of *moldavica*). Also there is this doubtful intermediate record of a specimen of *rakosiensis* from the Slavonian lowlands of former Yugoslavia (MÉHELY 1911, DELY 1986), but see above, under *rakosiensis*.

The fossil record – Palaearctic vipers

Conclusively the separation of the *ursinii s. l.* lineage from other Palaearctic viperines is estimated to have taken place about ten million years before present, i.e. during the Miocene (HERRMANN *et al.* 1987, 1992), based on immunological distances. The lineage consisting of the *berus* and *ursinii s. l.* groups ("*Pelias*" – sensu CHKHIKVADZE & ZEROVA 1983, ZEROVA 1992, NILSON & ANDRÉN 1997) is traced back to the lower Miocene with a large series of well-documented fossil



Fig. 69. The distribution of the different south and west European taxa of the *ursinii* complex, based on localities from literature. Some probably extinct populations of *rakosiensis* marked with questionmarks. The remaining and disjunct occurrence of *rakosiensis* is at present restricted to areas within the political borders of Hungary

records (SZYNDLAR 1984, 1991). The exact branching point between the *ursinii s. l.* lineage and the rest of "*Pelias*" has not been possible to demonstrate from fossil records up to present. But according to several phylogenetic reconstructions (phenetic – SAINT GIRONS 1980, immunological distances – HERRMANN *et al.* 1987; hierarchical cluster analysis, distance Wagner procedure – Herrmann *et al.* 1992) *ursinii s. l.* has branched off at a very early stage, in fact as an early sister-group to the rest of "*Pelias*" and *Vipera* (s. str.) (HERRMANN & JOGER 1997). The splitting of the main lineages of Palaearctic vipers, including "*Pelias*" (with *ursinii s. l.*) and *Vipera* s. str (*aspis/ammodytes* groups) actually goes back to lowermost



Fig. 70. The distribution of the different west Asian mountain taxa as here recognized. Based on known localities from literature. The distribution of *Vipera darevskii* is indicated by a black dot

Miocene, more than 20 million years ago (see NILSON & ANDRÉN 1997, for a review).

In this perspective, the actual splitting of the *ursinii* s. l. lineage may have taken place much earlier than in upper Miocene as was estimated by the biological clock (see above). Even an older origin of the whole *'ursinii'* branching event can not be ruled out. A reconsideration of placing the *ursinii* complex as a separate subgenus has been postulated (NILSON *et al.* 1999*a*). The name *Acridophaga* REUSS,1927, is available.

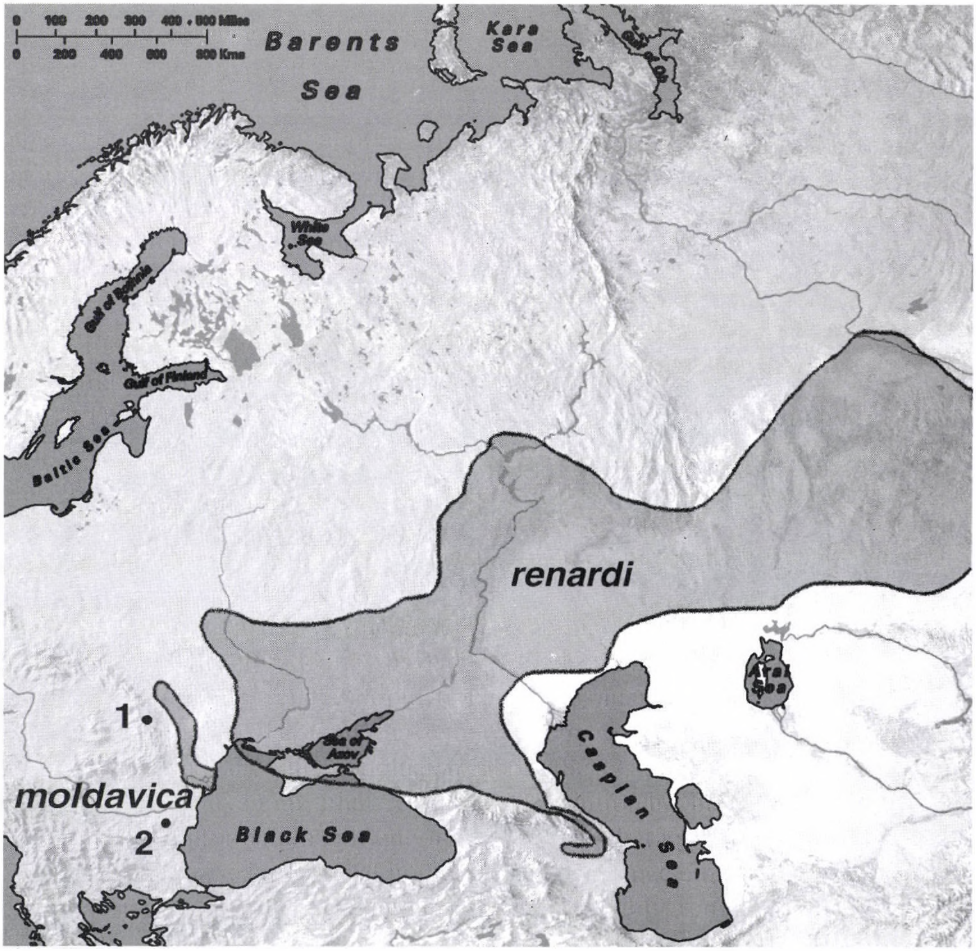


Fig. 71. The distribution of the lowland *Vipera 'u.' moldavica* and *V. renardi* (=mainly 'west-*renardi*'). Based on known localities from literature. Number 1 is the *moldavica* population from Mt. Rarau, Carpathians, and number 2 is the *moldavica* population from Sumen, Bulgaria

Hypothetical scenario

The members of the *ursinii* complex are restricted to dry meadow/steppe habitats, and the historical alterations in climate can help to understand the distribution patterns within this complex.

During the Turolian age (NM11) at about 8 million years ago, immigrants of various Asian steppe-elements indicate advancing dry biotas in Europe. At this time West Europe and the Mediterranean were woodlands and more humid and with warm climate.

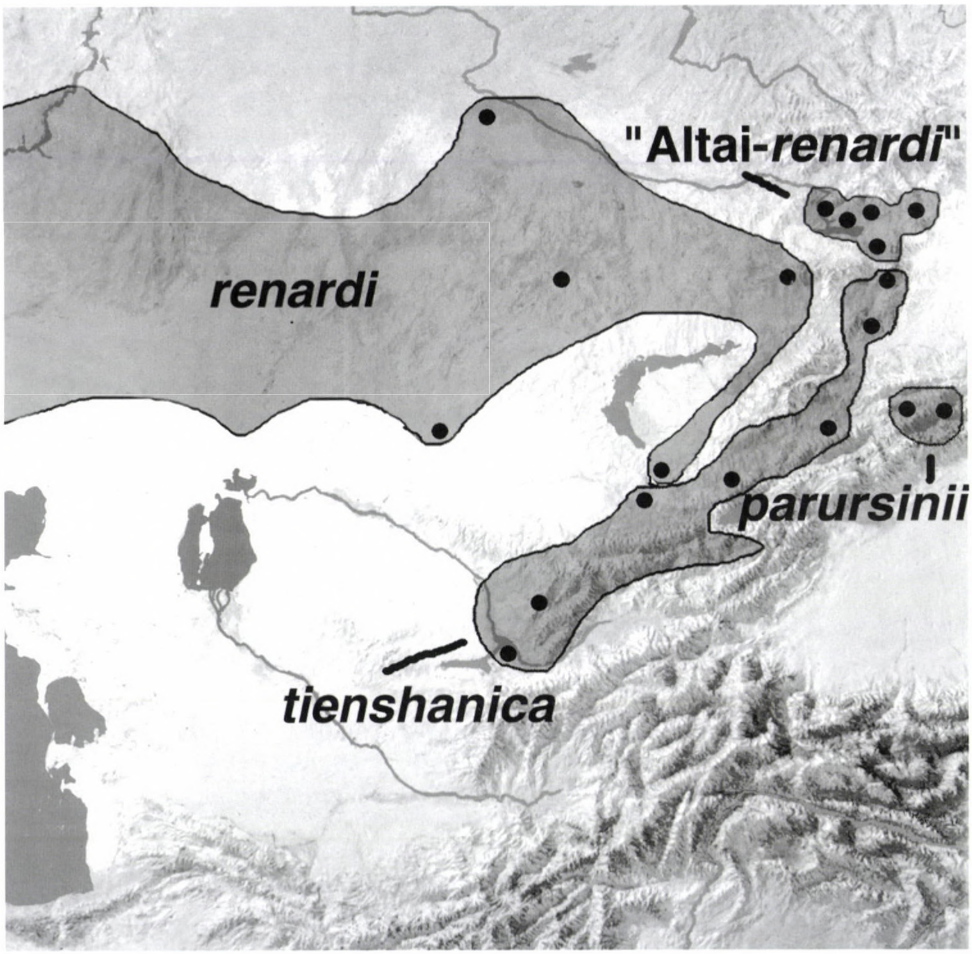


Fig. 72. The distribution of the different central Asian taxa as here recognized. Partly based on localities from literature, partly on own studies (= filled dots). *Vipera renardi* represents the populations refered to as 'east-*renardi*' in the text

During the Messinian salinity crisis (MN 13) at the end of Miocene, strong fluctuations between short, warmer and cooler phases took place. Continental climate, with decreasing humidity and temperature, resulted in extension of sclerophyllous evergreen woodlands around the Mediterranean. Continentalisation continued with a relative decrease in humidity during this period.

The Mediterranean basins were entirely flooded in the early Pliocene with the opening of the Strait of Gibraltar. The transgression also reached the Ponto—Caspian region. The climatic conditions again went warm and humid in the entire circum-Mediterranean area, and the humidity increased in Western, Middle and Eastern Europe.

The upper Pliocene was dominated by rapid climatic oscillations. In general, the climate turned arid. This period was characterised by the occurrence of large grass-browsing mammals, like *Mammuthus*, *Leptobos* and *Equus*, which tells us that grass-steppe habitats were predominating.

The climatic oscillations from the Pliocene continued into the early Pleistocene, which began with cooler and drier conditions. The temperature was slightly lower than today in Central Europe. The loess steppe expanded into Western Europe. In the middle Pleistocene (Biharian age) a steppe belt stretched across Europe and Asia. This phase is characterised by a pronounced rapid spreading of *Microtus* and related voles along the entire steppe zone. These rodents show an identical grassland-steppe habitat preference as the lowland *ursinii* taxa (*rakosiensis, renardi*, and *moldavica*).

In the upper Biharian age, an increase in humidity took place, and the following reforestation split the large steppe areas. This trend has continued from middle Pleistocene until today, with an accelerated alteration of cold and warm periods (STEININGER *et al.* 1985).

The following scenarios of the evolutionary history (although hypothetical) of the *ursinii* complex may be reconstructed:

The adaptations to subalpine and alpine climates could have taken place mainly during the different Pliocene–Pleistocene glacial periods. During the Pliocene, the climate was warm only to be followed by cold Pleistocene glacials. The species was certainly adapted to the Eurasian steppe/grassland habitats during the upper Miocene-Pliocene warmth period, and perhaps abundant and well spread in those puszta and steppe habitats which we know occurred during that period (STEININGER & RÖGL 1984). This would represent a first large occurrence in dry lowland areas.

When the cold invasions took place during Pleistocene the range of the species certainly decreased, and was perhaps restricted to a number of refuge areas between permanently glacial regions in different parts of Eurasia. Some refuges,

such as the Caucasus, were already established in the Pliocene. These refuges became colder, and similar to the alpine meadows that we can find in mountain ridges today (and where alpine *ursinii* s. l. occurs). Several of these Pleistocene isolated populations probably got adapted to the severe climatic conditions, while others did not and vanished. This may have taken place a number of times during the last four Pleistocene glacial – interglacial oscillations and at a number of places in Europe and Asia. Any population that did not adapt to colder conditions would become extinct in those parts of Eurasia that was submitted to these severe climatic fluctuations. During such conditions, the subalpine and alpine populations would be established.

In lowland Central Europe and Asia, areas with continuous continental climatic conditions prevailed also during the Pleistocene. These areas were refuges and later dispersal centres for warm-adopted species as has been shown for e.g. *Lacerta agilis* (JABLOKOV *et al.* 1980). *Lacerta agilis* and *Vipera ursinii* s. l. have almost identical and sympatric distributions in Asia and East Europe (except for the north and west of the range of the lizard). The taxon *graeca* is syntopic with *Lacerta agilis bosnica* in Greece (NILSON & ANDRÉN 1988), and *eriwanensis* and *Lacerta agilis brevicaudata* are syntopic in eastern Turkey, *macrops* is syntopic with *L. agilis bosnica* in former Yugoslavia, etc.

Vipera ursinii s. l. certainly occurred and could have had a larger refuge in these central parts of Asia during Pleistocene, and survived here in its more ancestral, plesiomorphic warm-adopted lowland form. From these eastern areas, a second re-invasion by lowland *V. ursinii* s. l. could have taken place during late Pleistocene interglacials, or during the post-Pleistocene warm period. Dispersal to the present lowland steppe and puszta habitats in Asia and east Europe would occur.

Such an east-west immigration is in line with the immigration hypothesis of SZYNDLAR (1984), based on fossil snake material. In addition, the opinion of MÉHELY (1911) and SCHWARZ (1936), that the European alpine populations were ancient relict populations, agree with this theory. The second wave (of lowland) *Vipera ursinii* s. l. probably never had the time, or possibility due to extensive forestation, to invade the whole original range. Today in westernmost Europe, only those relict populations that had remained from earlier immigrations, and got adapted to cold climate occur. The forestation of larger areas in those times might have functioned as an effective dispersal barrier for Quaternary lowland populations (as is the case today). This might have resulted in the present mosaic distribution of the lowland and alpine populations in Europe and Asia. The main Holocene distribution of the lowland populations is towards north and the main distribution of the alpine populations is towards south.

The lowland and alpine groups of populations do not reproduce with each other as they are ecologically separated (climatic preference and ecological niche) and act biologically as different species. In these aspects, they are rather much like the *Vipera kaznakovi – V. dinniki* complex in the Caucasus. Here the cold-adapted refuge populations (*dinniki*) never seem to adapt backwards and are restricted to the alpine meadows where they are found today (NILSON *et al.* 1994, 1995).

Ecological comparisons

Preferred habitat for all meadow vipers is dry grassland. This is a general characteristic of the habitat choice and it varies from alpine meadows to lowland grass steppe or dry puszta, but always grassland ecosystems. The *ursinii* complex is a basal sister taxon to the rest of the Eurasian vipers and it branched of at an early stage in the evolution of this lineage (Fig. 68). The evolution of the *Acridophaga* lineage from the early Miocene coincides with the origin and evolution of grasses and grassland ecosystems, a floristic event that reached its full ecological potential for the first time in the early Miocene (STANLEY 1993). The old age of the *ursinii*

Table 48. Altitudinal span for different taxa in the *V. ursinii* complex

Taxa	Altitude (m)	Reference
V. ursinii	900–2400	LEPRI 1923, ANGEL 1946, KRAMER 1961, BRODMANN 1987, CAPULA & LUISELLI 1992, own obs.
V. u. macrops	50 (Krk), 1000–2300	WERNER 1897, KRAMER 1961, BRODMANN 1987, own obs.
V. u. graeca	1750–2000	own obs.
V. u. rakosiensis	120–385	KRAMER 1961, KORSÓS *et al.* 1997, own obs.
V. u. moldavica	0–250 (900)	BRODMANN 1987, KORSÓS *et al.* 1997 own obs.
V. renardi	0–600* (1250)	own obs.
V. r. tienshanica	1030–2750	CAS, BMNH
V. renardi taxon (Altai form)	218–327	own obs.
V. r. parursinii	660–1300	ZHAO & JIANG 1979
V. anatolica	1700–2200	BRODMANN 1987, own obs.
V. eriwanensis	1700–2800	BRODMANN 1987, TEYNIE 1987 ALEKPEROV 1982, own obs.
V. ebneri	1500–3000	WETTSTEIN 1952, KRAMER 1961, own obs.
V. lotievi	1200–2700	GNM, ZISP

* Earlier authors often set the upper altitudinal range for *V. renardi* to between 2000 and 3000 m. However, that includes taxa here separated as *V. r. tienshanica, V. lotievi* and V. *eriwanensis*

complex is clearly reflected in the pronounced grassland adaptation that persists within this complex. The altitudinal distribution of the different taxa is markedly lowland or alpine/subalpine (Table 48), but always connected to dry grassland habitats. It is absent from all forested areas. The complex is covering a geographical area that is rather large and which is ranging from Western Europe to Central Asia (Figs 69–72). Within this huge range, the members of this complex use a number of different grassland habitats. The only exception as we can see, is the 'Altai form of *renardi*', which prefers rocky slopes, especially scree formations and moraines (own observations).

Reproductive pattern

Vipera ursinii s. l. is ovoviviparous and, like other vipers, gives birth to the young in August or September. Clutch size varies from relatively few in mountain alpine and subalpine taxa like *graeca* (range 2–3; NILSON & ANDRÉN 1988), *ursinii* (range 1–7, X=4.03; BARON *et al.* 1996) and *tienshanica* (range 1–6; PARASKIV 1956) to several (19–22) in lowland taxa like *rakosiensis* (JANISCH 1993, BOULENGER 1913) and up to 28 in *renardi* (KOTENKO 1989). However, the lowland 'Altai form of *renardi*' also has a rather low clutch size (3–12, N=4; own observations).

The French populations of *ursinii* are characterised by having the "*berus*-strategy" in breeding pattern (SAINT GIRONS 1980, 1982), i.e. spring mating triggered by the spring moult, and a strict spring spermiogenesis. At least *renardi* shows occasionally an autumn breeding pattern, i.e. the "*aspis*-strategy", with both autumn and spring spermiogenesis (NILSON & ANDRÉN 1989, 1997).

The lowland taxa like *rakosiensis* and *renardi* are growing larger. By having a larger clutch size and potentially a different reproductive system, members of the lowland and mountain populations act biologically like separate species. Also the 'Altai form of *renardi*', which is a lowland taxon, but with 'mountain' morphology, produces occasionally larger clutches. A female from the Saur Mountains gave birth to 12 young (own observation).

The bigger taxa like *rakosiensis* and *renardi* give births to larger clutches and apparently show potentially different reproductive systems. Additional research on the reproductive biology is necessary, but if this scenario can be verified, it would strongly support the hypothesis that members of the lowland and mountain populations are biologically completely different species.

Population size and genetic stress

Seven populations of *Vipera ursinii graeca* are known in the Pindos massive. Distances of several km, and deep valleys separate each of these from the others with quite different climate and habitat type. The populations seems to be effectively isolated from each other with reduced or no gene flow taking place. The size of each habitat is perhaps between two and ten hectares and rough estimate of the adult numbers in each population is around 50 individuals. Fifty pairs give a loss of 0.5 percentage heterozygosity per generation. The effective population size needs to be 500 adults for a probable long time survival (FRANKEL & SOULÉ 1981). If the populations of *graeca* have been of similar size for a large number of generations, which is a reasonable guess, they should contain no heterozygosity any more. Consequently, they should have reduced possibilities to respond to environmental changes by adaptations due to homozygosity. It is a loss of adaptability caused by the conditions that they have been living in too small population for too long, and a climatic shift, such as the "green-house effect", can have a serious effect on these populations. If this scenario is real, there could be a great risk that *graeca* is approaching extinction. The situation could be the same for several of the isolated mountain populations in former Yugoslavia and in Italy and France. It could have been the reason for the obvious disappearance of meadow vipers in Bulgaria and at Mt. Rarau in Romania, as well as the reason for the scarcity of *anatolica* in the Ciglicara area.

The *ursinii* populations are in several cases much endangered and of small size. In more recent times the more widely distributed lowland populations have also been fragmented by agriculture and human activities of different kinds, and are also facing the risk of genetic impoverishment.

For genetic studies, it is necessary to use fresh tissues, but for conservation reasons, it is neither possible nor advisable to collect wild specimens. Consequently, it is not possible to estimate the degree of heterozygozity based on traditional electrophoretic methods. However, the idea of morphological asymmetry as an indicator of homozygosity (SOULÉ 1979) can be used to some extent and thereby give us an indication of what populations might have lost in heterozygozity (Table 49).

All populations showed low asymmetry in at least one character. Most (eleven) had low asymmetry in two characters, while six had low asymmetry in three. Only two populations had low values in all four characteristics, while four populations had only one character with low value. The two populations with low values in all characters, and supposedly showing high heterozygozity both belonged to *renardi* (the Dnjepr (Ukraine) and Dzherzkazgan (Kazakhstan) populations). These are populations from regions with large distributions of suitable habi-

tats, at least until recently. The Dnjepr river valley population is at present surrounded by intensive agriculture areas, but has until recently been in contact with other *renardi* populations in the South Ukrainian steppes. The second population, from Kazakhstan, is supposed to be in dense numbers in good steppe habitats.

The four populations with three of four characteristics highly asymmetric are Cemerno (*macrops*), Grammat/Neusiedl (*rakosiensis*), and two *eriwanensis* populations (Sarakamis and Ara-Iler). However the *eriwanensis* populations are rather

Table 49. Percentage of asymmetry in selected morphological traits in populations when six or more specimens have been available. Italic figures are below the mean value =low asymmetry (presumed higher heterozygosity). Bold figures are above the mean value, and show comparatively high degree of asymmetry (presumed low heterozygosity)

Taxon	Population	N	Supralab	Sublab	Circum-oculars	Loreals	Total high	Total low
V. ursinii	Mt. Ventoux	6	*16*	*17*	*33*	**83**	*3*	**1**
	Mt. de Lure	16	*6*	*25*	56	63	*2*	
	Mt. Sibillini	19	32	*6*	*44*	*44*	*3*	
	Gran Sasso	7	*0*	29	57	*1*	*2*	
V. u. macrops	Korita	16	*13*	*24*	**75**	66	*2*	**1**
	Cemerno	7	**50**	33	*50*	66	*1*	**1**
	Baba Planina	14	*7*	**62**	58	*50*	*2*	**1**
V. u. graeca	Pindos	14	*15*	*7*	69	*46*	*3*	
V. u. rakosiensis	Gram.Neusiedl	9	**44**	*11*	**75**	**89**	*1*	**3**
	PeszéradSorok	12	*17*	*33*	*42*	*42*	*3*	
	Dabas	21	33	*20*	67	*43*	*2*	
	Kunpeszér	8	25	*12*	*50*	*44*	*3*	
V. u. moldavica	Valea l.David	15	36	*20*	54	*50*	*2*	
	Romanesti	17	35	**65**	*47*	*41*	*2*	**1**
V. renardi	Ile Orlov	8	*0*	*11*	55	63	*2*	
	Dnjepr	13	*15*	*23*	*38*	*50*	*4*	
	Dzherzkazgan	10	*20*	*20*	*50*	*30*	*4*	
V. lotievi	Armhi-Madxal	14	*18*	31	*38*	62	*2*	
V. ebneri	Lar valley	15	27	40	*33*	*47*	*2*	
V. eriwanensis	Sarakamis	11	27	**55**	*45*	54	*1*	**1**
	Kagizman	7	*14*	*14*	**71**	*43*	*3*	**1**
	Ara-Iler	17	*6*	35	53	53	*1*	
V. r. parursinii	Nilka Xian	26	23	42	*31*	*50*	*2*	
Mean value			21	28	52	51		

close to the mean value in several characteristics and it is difficult to explain loss of heterozygosity in these rather dense populations occurring in large regions of good habitats, and several adjacent populations nearby. It is perhaps not reflecting an accurate situation in this case. The Cemerno population in Bosnia-Herzegovina is morphologically different from typical *macrops*, and shows several similarities with its lowland relative *graeca*, and may be a result of long inbreeding, and loss of heterozygosity. In addition, the Grammat/Neusiedl population (*rakosiensis*) in Austria can have been a result of low population density and inbreeding before it finally became extinct.

In the same way, a few populations have an unusually high percentage of asymmetry in one or more characters, indicating low degree of heterozygosity. Seven populations show high numbers in one character. A single population, again Grammat/ Neusiedl in Austria, have unusually high values in three of the four characters, enhancing the picture of being a genetically poor population during the last period of its existence. The investigated specimens were collected in 1953.

The Sarakamis and Cemerno populations, again, are amongst the ones with high value character, while the other five are Mt. Ventoux (*ursinii*), Korita and Baba Planina (*macrops*), Romanesti (*moldavica*), and Kagizman (*eriwanensis*). All except *moldavica* are alpine populations, and it is not possible to say whether it is a true loss of heterozygosity or just coincident. The same is of course true for the Moldavian lowland population. We know that these Romanian populations are extremely small, surrounded by intensive agricultural activities and monocultures. It is reasonable to suspect a true inbreeding and genetic loss in this case, probably comparable with the Grammat/Neusiedl population, and as can be suspected to be the true situation for several other isolated lowland populations. One example is the *rakosiensis* population at Ócsa, Hungary, with a high degree of abnormal characteristics compared to the nearby Dabas population (DELY & STOHL 1984). The latter is a comparatively large population; while the former has a much-reduced amount of suitable habitats left and is probably extinct (own observations).

In some cases, like for the Austrian *rakosiensis*, loss of genetic variation can have played an important role in the extinction process in a rapidly changing environment. On the other hand, the Pindos sample (*graeca*), as several presumed small and isolated mountain populations, does not show any high depression of heterozygosity in this test.

Future – ursinii *conservation strategies*

It is of great importance to perform detailed studies focusing on or below the level of conventional taxonomic species, to provide information of immediate help in conservation biology. The situation in the *ursinii* complex (e.g. JOGER *et al.*

1992) clearly demonstrates this by indicating that most (perhaps all) of the small, isolated and declining populations of meadow vipers represent unique genetic entities which deserve strict protection.

The main objective must be to protect viable populations of *Vipera ursinii* s. l. and their environment. However, in species protection we must also include the maintenance of the genetic diversity represented by the species. Hereby unique isolated populations must be considered. To protect biological or genetic diversity motivated both for ecological and ethical reasons, it is necessary to focus more on the protection of diversity to make possible a future evolution and adaptation of animals and plants to a changing environment.

Taxonomy must reflect the phylogeny. Taxa, such as species and subspecies are terminal ends of phylogenetic lineages. Each taxon has its own unique gene pool, which must be recognised and protected from extinction. Taxa have split off from common ancestors at variable times and are more or less distinctly related to each other. Also taxa have been subjected to more or less strong selection and are more or less modified from each other in morphological traits. As is the case in *Vipera ursinii* s. l., closely related populations can appear different and distinctly related taxa can show a phenetic similarity (i.e. *parursinii* and *rakosiensis*). Historically we have placed taxa in species and subspecies categories based on morphology. Modern studies of genetic compositions and distances in and between taxa show that traditional taxonomy is not always in accordance with genetic integrity and the underlying phylogenetic process. We must therefore protect and save threatened, genetically unique populations no matter if they are referred to species or subspecies categories in a traditional sense. The taxonomy of *Vipera ursinii* s. l. has changed dramatically in recent years as more groups have been investigated with modern genetic methods. For these reasons, it is not appropriate to base a conservation program only on the traditional morphological taxonomy. Instead, we should focus our conservation activities on genetically unique terminal taxa (species or subspecies) that are endangered.

What sort of future can be predicted for *Vipera ursinii*? Serious – if much recent literature and appeals in conservation are considered. In recent times *Vipera ursinii* s.lat. has been included in CITES, which however is only of major importance if there is a commercial threat. This, however, must be considered as relatively small (Although, a large series of "*V. ursinii ebneri* from Alma Ata" (=*tienshanica*) was offered for sale in the Netherlands in 1992 during a commercial "snakeday"). If trade will become a real threat, it must be a result of preceding destruction of the populations by e.g. habitat destruction, pollution, draining or other habitat alterations. This would have pressed down the population sizes towards a critical level. Then collecting of individuals becomes a hazard for the pop-

ulation. Such a critical situation is first archived for the lowland taxa occurring in meadow and steppe habitats i.e. *rakosiensis* and *renardi*. These taxa occur in habitats that can easily be altered in a serious way. *Vipera 'u.' rakosiensis* seems nowadays to be restricted to four reproducing populations in Hungary. Of these, one is found in Hanság, not far from the Austrian border. The remaining three are from the regions south of Budapest, from the Bugac Puszta at the Kiskunság National Park in the south to the regions of Dabas and Kunpeszér further north. The main reason for their decline in some areas and the extinction in others seems to be the intensive agricultural activity in the habitat (Fig. 73). The most serious threat to the remaining populations seems to be preparatory agricultural work, such as draining of wet meadows, cutting, burning (Fig. 76), and grazing by sheep and geese. In these areas collecting by pet keepers and killing by shepherds and farmers may be serious problems (CORBETT 1989, FÜLÖP 1992, STUMPEL *et al.* 1992). One of the very few remaining Hungarian (and world) populations of this taxon was recently (1997) destroyed by man burning the entire site (ÚJVÁRI *et al.* 1998).

The Romanian population of *rakosiensis* at Cluj in Transsylvania has obviously become extinct in recent times (VANCEA *et al.* 1985, KORSÓS *et al.* 1997) due to agricultural activities. This is the case also for Austria (CORBETT 1989, CABELA & TIEDEMANN 1985, KAMMEL, 1992*a*). In Hungary, the habitat fragmentation through large monocultural fields prevents any increase or even jeopardises the survival in the end for the remaining populations. In Eastern Romania, the situation is extreme, where enormous monocultural fields cover almost entire Moldavia, where *moldavica* was probably once more widespread. Today, it has its perhaps last remaining groups of individuals at Jasi and in the Danube Delta. Survival for any longer time is unlikely if agricultural policy continues as at present.

The alpine populations are also locally threatened by various factors, including habitat destruction (Conservation Committee (SEH) 1987, BRUNO & MAZZEI 1987, CORBETT 1989, GROOMBRIDGE, pers. com., CAPULA & LUISELLI 1992), but for these populations collecting might be the more severe threat. Still locally, populations show a high density, and this is especially pronounced at localities that are still not known to a larger public.

The future survival of vital populations of *ursinii* s. l. over major parts of its range will consequently depend on our success in restoring large enough habitats, which meet the basic ecological demands of these snakes. In most cases, this is an obvious reason that can explain the loss or decline of populations. Those living in lowland grasslands are most threatened because of the conflict with agriculture economic interests. An optimal habitat demands a natural fluctuating water regime, which creates the necessary ground microclimate and structure. Such areas have a mosaic of wet and dry patches and high tussocks with withered grass; they

also have hiding places and invertebrate prey. Large protected areas, where the former natural ground water level and natural fluctuation is allowed is therefore a first important step. In many cases well-balanced grazing can be allowed, but not modern grass cutting where the varying ground structure, including the tussocks, are removed. Large parts of the Asian nutrition-poor steppe habitats have been turned into agriculture areas with the help of fertilisers. To get back habitats good enough for *ursinii* taxa these areas must be left free for vegetation development so that the natural structure with patches of ground cover and tussocks is coming back. In these habitats, grazing can be a serious problem. Our analysis of the *ursinii* complex clearly shows that we are dealing with a number of different evolutionary entities and therefore conservation measure to safeguard vital populations are highly recommended over the entire range.

*

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REFERENCES

AGER, D. V. (1980) *The Geology of Europe*. McGraw-Hill Book Company Ltd. London.

AGRIMI, U. & LUISELLI, L. (1992) Feeding strategies of the viper Vipera ursinii ursinii (Reptilia, Viperidae) in the Appennines. *Herpetol. J.* **2**: 37–42.

ALEKPEROV, A. M. (1978) *Amphibians and reptiles of Azerbaijan*. Baku, Azerbaydzhan S. S. R., Elm Publishers, 264 pp. [In Russian]

ALEKPEROV, A. M. (1982) The present state of rare and threatened species and subspecies of herpetofauna in Azerbaidzhan. *Vertebr. Hung.* **21**: 19–24.

ALIEV, T. R. & GANIEV, F. R. (1985) Distribution and ecological-morphological peculiarities in the meadow viper, Vipera ursinii Bonaparte, 1835 in Azerbaidjan. *Izv. Akad. Nauk AZSSR, Ser. Biol. Nauk*, pp. 44–50. [In Russian]

ANANJEVA, N. B., MUNKHBAYAR, KH., ORLOV, N. L., ORLOVA, V. F., SEMENOV, D. V. & TERBISH, KH. (1997) *Amphibians and reptiles of Mongolia*. KMK Ltd, Moskow, 416 pp. [In Russian]

ANDRÉN C. & G. NILSON (1979) Vipera latifii, an endangered viper from Lar Valley, Iran, and remarks on the sympatric herpetofauna. *J. Herpetol.* **13**(3): 335–341.

ANGEL, F. (1946) Reptiles et Amphibiens. *Faune de France*, **45**: 1–204.

ARNOLD, S. J., REAGAN, N. L. & P. A. VERRELL (1993) Reproductive isolation and speciation in Plethodontid salamanders. *Herpetologica* **49**(2): 216–228.

BANNIKOV, A. G., DAREVSKY. I. S., ISCENKO, W.G., RUSTAMOV, A. K. & N. N. SCERBAK (1977) *Opredelitjel zemnovodnych i presmykajushchichsja fauny SSSR*. Moscow (Prosveshchenije), 415 pp.

BARAN, I. (1976) Türkiye Yilanlarinin Taksonomik Revizyonu ve Cografi Dagilislari. *TBTAK Yayinlari* No 309, T.B.A.G. seri no 9, Ankara, 177 pp.

BARAN, I. & M. K. ATATÜR (1998) *Turkish herpetofauna (Amphibians and Reptiles)*. Ankara, 1–214.

BARON, J.-P. (1987) La Vipére d'Orsini (Vipera ursinii Bonaparte, 1835). Systematique, distribution géographique et habitat la population du Mont Ventoux (Vaucluse). *Études Vauclusiennes*, **3**: 127–134.

BARON, J.-P. (1992) Régime et cycles alimentaires de la Vipére d'Orsini, Vipera ursinii ursinii (Bonaparte, 1835) au Mont Ventoux, *France. Rev. Ecol.* **46**: 11–35.

BARON, J.-P., FERRIÉRE, R., & H. SAINT GIRONS (1993) Différenciation morphologique de quatre populations Francaises de Vipera ursinii ursinii Bonaparte, 1835 (Reptilia, Viperidae). *Revue Suisse de Zoologie* **100**(1): 187–196.

BARON, J.-P., FERRIÉRE, R., CLOBERT, J. & H. SAINT GIRONS (1996) Stratégie démographique de Vipera ursinii ursinii au Mont-Ventoux (France). *C.R.Acad. Sci. Paris, Life Sciences*, **319**: 57–69.

BASOGLU, M. (1949) On some varities of Vipera berus from the extreme North-eastern Anatolia. *Rev. Fac. Sc., Univ., Istanbul* **12**(3): 182–190.

BASOGLU, M. & I. BARAN (1980) *Turkiye surungenleri, kisim II. Yilanlar*. Bornova–Izmir, IX+218 pp.

BESKOV, W. (1973) Über die subgenerische Zugehörigkeit der Bulgarischen Vipera ursinii (Bonaparte, 1835) (Serpentes). *Bull. de l'Institut de Zoologie et Musée, Académie Bulgare des Sciences* **37**: 103–112.

BESKOV, W. & P. BERON (1964) *Catalogue et Bibliographie des Amphibiens et des Reptiles en Bulgarie*. Sofia (Acad. Bulg. Sci.), 39 pp.

BEA, A., F. BRANA, J. P. BARON & H. SAINT GIRONS (1992) Régime et cycles alimentaires des Vipères européennes (Reptilia, Viperidae). Etude comparée. *Ann. Biol.* **31**(1): 1–44.

BILLING, H. (1985) Beschreibung eines weiteren Exemplares von Vipera ursinii anatolica Eiselt and Baran, 1970 (Serpentes: Viperidae). *Salamandra* **21**: 95–97.

BILLING, H., NILSON, G. & U. SATTLER (1990) Vipera pontica sp. n., a new viper species in the kaznakovi group from northeastern Turkey and adjacent Transcaucasia. *Zoologica Scripta* **19**(2): 227–231.

BOGDANOV, O. P. (1960) *Fauna of Uzbekistan*. Acad. Sci. Uzbekistan CCP, Taskent **1**: 1–159. [In Russian]

BOLKAY, S. (1924) A list of the Amphibians and Reptiles preserved in the Bosnian-Hercegovinan Land-Museum with morphological, biological and zoogeographical notes. *Spomenik Srpske Kraljewske Akademije* **61**: 1–39.

BONAPARTE, C. L. (1835 (1832–1841)) Iconografia della Fauna Italica per le quatro classi degli animali vertebrati, II Amfibi. *Roma Dalla Tipografia Salviucci* **12**: 155–204.

BORKIN, L. J., MUNKHBAYAR, KH., ORLOV, N. L., SEMENOV, D. V. & KH. TERBISH (1990) Distribution of reptiles in Mongolia. *USSR Acad. Sci. Proc., Zool. Inst., Leningrad* **207**: 22–138.

BOULENGER, G. A. (1893*a*) On a little-known European Viper, Vipera ursinii, Bonap.. *Proc. Zool. Soc. London* **51**: 757–760.

BOULENGER, G. A. (1893*b*) On Vipera renardi, Christoph. *Proc. Zool. Soc. London* **51**: 757–760.

BOULENGER, G. A. (1913) *The snakes of Europe*. London, Methuen and Co., 269 pp.

BRELIH, S. & G. DZUKIC (1974) *Catalogus Faunae Jugoslaviae – Reptilia.* Ljubliana **4**(2): 1–32.

BRODIE III, E. D. & T. GARLAND, JR. (1993) Quantitative genetics of snake populations. Pp. 315–362. *In* SEIGEL, R. A. & J. T. COLLINS (Eds.) *Snakes – Ecology & Behavior.* McGraw-Hill Inc.

BRODMANN, P. (1987) *Die Giftschlangen Europas und die Gattung Vipera in Afrika und Asien.* Kümmerly+Frey, Bern. 148 pp.

BRUNO, S. (1967) La Vipera ursinii (Bonaparte 1835) in Italia. *Mem. Mus. Civ. Stor. Nat. Verona* **15**: 105–125.

BRUNO, S. (1980) L'erpetofauna delle isole de Cres, Trstenik, Plavnik e Krk (Kvarner, Jugoslavija). *Atti Mus. civ. Stor. nat. Trieste* **31**(3): 249-282.

BRUNO, S. & P. MAZZEI (1987) Lista rossa dei rettili italiani. La Vipera di Orsini (Vipera ursinii). *Ambiente e Natura* **3**(1): 16–19.

BURESCH, I. & J. ZONKOW (1932) Die Verbreitung der Giftschlangen (Viperidae) in Bulgarien und auf der Balkanhalbinsel. *Arb. bulgar. naturf. Ges. Sofia.* Bd. 15–16: 189–201.

BURESCH, I. & J. ZONKOW (1934) Untersuchungen über die Verbreitung der Reptilien und Amphibien in Bulgarien und auf der Balkanhalbinsel. 2. Schlangen (Serpentes). *Mitt. Königl. naturwiss. Inst., Sofia* **7**: 106-188.

CABELA, A. & F. TIEDEMANN (1985) Atlas der Amphibien und Reptilien Österreichs (Stab´nd 1984). *Neue Denkschriften des Naturhistorisches Museum in Wien* **4**: 1–80.

CAPULA, M. & L. LUISELLI (1992) Distribution and conservation of Vipera ursinii (Reptilia: Viperidae) in Italy. *Proc. Sixth Ord. Gen. Meet. S.E.H., Budapest 1991,* pp. 101–105.

CASTANET, J. (1978) (Hrsg.) *Atlas préliminaire des Reptiles et Amphibiens de France.* Montpellier, 137 pp.

CHERNOV, S. A. (1939) Herpetological Fauna of Armenia and Nahichevan. *Assr. Sbornik Akad. Nauk. Armenian* SSR **7**: 77–194. [in Russian]

CHKHIKVADZE, V. M. & G. A. ZEROVA (1983) The morphology of thoracal vertebrae & systematic position of some viperine snakes. *Bull. Acad. Sci. Georgian SSR* **112**(3): 653–656. [in Russian]

CHONDROPOULOS, B. P. (1989) A checklist of Greek reptiles. II. Snakes. *Herpetozoa* **2**(1–2): 3–36.

CHRISTOPH, H. (1861) Pelias renardi, mihi. *Bull. Soc. Imp. Natural. Moscou* **34**(2): 601–606.

CITA, M. B. (1982) The Messinian salinity crisis in the Mediterranean: a review. *In* BERCKHEMER, H. & K. HSÜ (eds) *Alpine, Mediterranean Geodynamics* **7**: 113–140.

CONSERVATION COMMITTEE (SEH) (1987) Identification of critical biotope sites for threatened amphibians and reptiles in Council of Europe member countries. *Amphibia–Reptilia* **8**(1): 88–91.

CORBETT, K. F. (1986*a*) Biogenetic reserves for threatened species of herpetofauna in Western Europe. Pp. 727–730. *In* ROCEK, Z. (ed.): *Studies in Herpetology*. Charles Univ., Prague. 754 pp.

CORBETT, K. F. (ed.) (1986*b*) *Report on the critical habitats of threatened European reptiles and amphibians.* Report nr. SN-VS (86) 5 and 6. Council of Europe, Strasbourg. 72 pp.

CORBETT, K. F. (ed.) (1989) *Conservation of European reptiles and amphibians.* Christopher Helm, London, 274 pp.

CORBETT, K. F. (1992–93) Viper conservation in Europe. Pp. 11–15. *In* JOHNSON, B. & V. MENZIES (eds) *International Symposium and Workshop on the Conservation of the Eastern Massasauga Rattlesnake Sistrurus catenatus catenatus.* Proc. Symp. Workshop, Metro. Toronto Zoo.

CRACRAFT, J. (1989) Speciation and its ontology: The empirical consequences of alternative species concepts for understanding of patterns and processes of differentiation. Pp. 28–59. *In* OTTE, D. & J. A. ENDLER (eds) *Speciation and its consequences*, Sinauer, Sunderland, Massachusetts.

CROTHIER, B. I., CAMPBELL, J. A. & D. M. HILLIS (1992) Phylogeny and historical biogeography of the Palm-Pitvipers, genus Bothriechis: Biochemical and morphological evidence. Pp. 1–19. *In* CAMPELL, J. A. & E. D. BRODIE (eds) *Biology of the Pitvipers*, Selva.

DAREVSKY, I. S. (1956) A new species of the venomous snake, Vipera kaznakovi Nikolsku, for the fauna of Armenia. *Bull. Acad. Sci. Armenia, Yerevan* **9**(12): 127–130. [in Russian]

DELY, O. G. (1978) Hüllők – Reptilia. *Fauna Hung.*, Budapest, **20**(4): 1–120.

DELY, O. G. (1983) Mikor jelent meg a parlagi vipera (Vipera ursinii rakosiensis Méhely) leírása? (Wann ist die Beschreibung von Méhely über Vipera ursinii rakosiensis erschienen?). *Állattani Közlemények* **70**: 117.

DELY, O. G. (1986) Megjegyzések a parlagi Vipera (Vipera ursinii rakosiensis Méhely, 1893) szlavóniai elterjedéséhez (Bemerkungen zum vorkommen der Spitzkopfotter (Vipera ursinii rakosiensis Méhely, 1893) in Slawonien). *Állattani Közlemények* **73**: 119–120.

DELY, O. G. (1987) Amphibians and reptiles of the Kiskunság. Pp. 404–425. In KASZAB, Z. (ed.) *Natural history of the national parks of Hungary, Vol. 5. The Fauna of the Kiskunság National Park.* Akadémiai Kiadó, Budapest.

DELY, O. G. & M. JANISCH (1959) La répartition des vipérs de champs (Vipera ursinii rakosiensis Méhely) dans le Bassin des Charpathes. *Vertebr. hung.* **1**(1):25–34.

DELY, O. G. & G. STOHL (1984) Weitere Beiträge zur Kenntnis des Vipera ursinii-Formenkreises (Viperidae). *Vertebr. hung.* **22**: 15–46.

DELY, O. G. & G. StOHL (1989*a*) Phylogenetische Probleme in dem Vipera ursinii-Formenkreises (Serpentes, Viperidae). *Vertebr. hung.* **23**: 9–20.

DELY, O. G. & STOHL, G. (1989*b*) Ergänzende Angaben zur Diagnose der Unterart Vipera ursinii ebneri Knoepffler et Sochurek, 1955 (Serpentes, Viperidae). *Vertebr. hung.* **23**: 21–27.

DIMITROPOULOS, A. (1985) First records of Orsini's viper, Vipera ursinii (Viperidae), in Greece. *Ann. Musei Goulandris* **7**: 319–323.

DIMOVSKI, A. (1964) Beitrag zur Herpetofauna Mazedoniens. *Fragmenta Balcanica* **5**(4): 19–22.

DOWLING, H. G. (1951) A proposed standard in counting ventrals in snakes. *Brit. J. Herpetol.* **1**: 97–99.

DUJSEBAYEVA, T. & A. KHAMITOV (1997) On the distribution of Orsini's Viper, Vipera ursinii Bonaparte, 1835 (Serpentes, Viperidae) in Kazakhstan: a review. *Abstr. First Internat. Symp. Snakebite, Zhanjiang, China.*

EDBERG, E. (1984) *Donaudeltat och Dobrogea.* Stockholm, 52 pp.

EISELT, J. (1976) Ergebnisse zoologischer Sammelreisen in der Türkei: Bemerkenswerte Funde von Reptilien, II. *Ann. Naturhist. Mus. Wien* **80**: 803–814.

EISELT, J. & I. BARAN (1970) Ergebnisse zoologischer Sammelreisen in der Türkei: Viperidae. *Ann. Naturhist. Mus. Wien* **74**: 367–369.

ENGELMAN, W.-E., FRITZSCHE, J., GÜNTHER, R. & F. J. OBST (1986) *Lurche und Kriechtiere Europas.* Ferdinand Enke Verlag Stuttgart, 420 pp.

FOX, W., GORDON, C. & M. H. FOX (1961) Morphological effects of low temperatures during embryonic development of the garter snake, Thamnophis elegans. *Zoologica* **46**(5): 57–72.

FRANKEL, O. H. & M. E. SOULÉ (1981) *Conservation and evolution.* Cambridge Univ. Press, 327 pp.

FROST, D. R. & D. M. HILLIS (1990) Species in concept and practice: Herpetological applications. *Herpetologica* **46**: 87–104.

FUHN, I. E. & S. VANCEA (1961) Reptilia. *In Fauna Republicii Populare Romine,* Vol. 14(2), 378 pp.

FÜLÖP, T. (1992) Distribution and conservation measures of the meadow viper (Vipera ursinii rakosiensis) in the Hanság Nature Reserve. *Proc. Sixth Ord. Gen. Meet. S.E.H.*, Budapest 1991, pp. 219–224.

GRILLITSCH, B., GRILLITSCH, H. HÄUPL, M. & F. TIEDEMANN (1983) *Lurche und Kriechtiere Niederoesterreichs.* Facultas – Verlag, Wien, 176 pp.

GOLAY, P., SMITH, H. M., BROADLEY, D. G., DIXON, J. R., MCCARTHY, C., RAGE, J. C., SCHÄTTI, B. & M. TORIBA (1993) *Endoglyphs and other major venomous snakes of the world.* Azemiops Herpetological Data Center publ., 478 pp.

HERRMANN, H.-W., JOGER, U., NILSON, G. & C. G. SIBLEY (1987) First steps towards a biochemically based reconstruction of the phylogeny of the genus Vipera. *Proc. Fourth Ord. Gen. Meet. S.E.H.*, Nijmegen 1987. Fac. Sci. Nijmegen, pp. 195–200.

HERRMANN, H.-W., JOGER, U. & G. NILSON (1992) Molecular phylogeny and systematics of viperine snakes I. General phylogeny of European vipers (Vipera sensu stricto). *Proc. Sixth Ord. Gen. Meet. S.E.H.*, Budapest 1991, pp. 219–224.

HERRMANN, H.-W. & U. JOGER (1997) Evolution of viperine snakes. *In* THORPE, R. S., WÜSTER, W. & A. MALHOTRA (eds) *Venomous Snakes – Ecology, Evolution and Snakebites. Symp. Zool. Soc., London* **70**: 43–61.

HÖGGREN, M., NILSON, G., ANDRÉN, C., ORLOV, N. L. & B. S. TUNIYEV (1993) Vipers of the Caucasus: Natural history and systematic review. *Herpetological Natural History* **1**(2): 11–19.

HONEGGER, R. E. (1981) Threatened amphibians and reptiles in Europe. Supplementary volume of "*Handbuch der Reptilien und Amphibien Europas*". Akademische Verlagsgesellschaft, Wiesbaden. 158 pp.

HORVATH, F. & H. BERCKHEMER (1982) Mediterranean backarc basins. *In* BERCKHEMER, H. & K. HSÜ (eds). *Alpine–Mediterranean Geodynamics. Geodynamics Series* **7**: 141–173.

HSÜ, K. J. & F. GIOVANOLI (1979) Messinian event in the Black Sea. *Paleogeogr., Paleoclimat., Paleoecol.* **29**: 75–94.

JABLOKOV, A. W., BARANOV, S. S. & A. S. ROZANOV (1980) Population structure, geographic variation and microphylogenesis of the sand lizard (Lacerta agilis). *In* HECHT, M. K. & W. E. STERRE (eds) *Evolutionary Biology.* Plenum Press, **12**: 91–127.

JANISCH, M. (1993) A mutant form of the meadow viper (Vipera ursinii rakosiensis Méhely) from Hungary with a peculiar colour pattern. *Miscnea zool. hung.* **8**: 45–49.

JOGER, U. (1984) *The venomous snakes of the Near and Middle East.* Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A, Nr. 12, 115 pp.

JOGER, U., HERRMANN, H.-W. & G. NILSON (1992) Molecular phylogeny and systematics of viperine snakes II. A revision of the Vipera ursinii complex. *Proc. Sixth Ord. Gen. Meet. S.E.H.*, Budapest 1991, pp. 239–244.

KAMMEL, W. (1992*a*) Zur Situation der Wiesenotter, Vipera ursinii rakosiensis (Méhely, 1894) (Squamata: Serpentes: Viperidae), in Niederösterreich. *Herpetozoa* **5**(1–2): 3–11.

KAMMEL, W. (1992*b*) Zur Situation der Wiesenotter, Vipera ursinii rakosiensis (Méhely, 1894), und der Pannonischen Bergeidechse, Lacerta vivipara pannonica Lac and Kluch. 1968, im Burgenland (Österreich). *Herpetozoa* **5**(3–4): 109–118.

KARAMAN, S. L. (1928) III Prilog herpetologiji jugoslavije (riass. francese). *Glasnika skopskog naucnog drustva, Skopje* **4**: 129–143.

KARAMAN, S. L. (1939) Über die Verbreitung der Reptilien in Jugoslavien. *Ann. Mus. Serbie Meridionalis* **1**: 1–20.

KNOEPPFLER, L. PH. & E. SOCHUREK (1955) Neues über die Rassen der Wiesenotter (Vipera ursinii Bonaparte). *Burgenl. Heimatblat* **17**(4): 185–188.

KORSÓS, Z. (1991) Európa legveszélyeztetettebb mérgeskígyója a parlagi vipera (Vipera ursinii rakosiensis). (The most threatened venomous snake of Europe: Vipera ursinii rakosiensis). *Természetvédelmi Közlemények* **1**: 83–88.

KORSÓS, Z. & T. FÜLÖP (1994) A parlagi vipera (Vipera ursinii rakosiensis Méhely, 1893) száz éve. (One-hundred years of the meadow viper (Vipera ursinii rakosiensis Méhely, 1893). *Állatt. Közlem.* **78**(Suppl.): 31–38.

KORSÓS, Z. & B. ÚJVÁRI (1998) A rákosréti vipera Kolozsvár környékén (The Hungarian Meadow Viper in the vicinity of Cluj). *Állatt. Közlem.* **83**: 123–128.

KORSÓS, Z. & B. ÚJVÁRI (1999) Situation of the Vipera ursinii species group in Romania and Moldova. *Abstracts Tenth Ord. Gen. Meet. S.E.H., Irakleio 1999*, pp. 85–86.

KORSÓS, Z., ÚJVÁRI, B. & ZS. TÖRÖK (1997) Searching for the meadow viper in Romania. *Miscnea zool. hung.* **11**: 77–88.

KOTENKO, T. I. (1981) On Vipera ursinii renardi in the south of Ukraine. *In* DAREVSKIJ, I. S., ANANEVA, N. B., BARKAGAN, Z. S ., BORKIN, L. YA., SOKOLOVA, T. M. SHCHERBAK, N. N. (eds) *The problems of Herpetology: abstracts.* Nauka, Leningrad, p. 73. [in Russian]

KOTENKO, T. I. (1989) Vipera ursinii renardi (Reptilia: Serpentes) in the Ukraine. *Abstracts, First World Congress in Herpetology*, Canterbury.

KOTENKO, T. I., MOROZOV-LEONOV, S. Y. & S. V. MEZHZHERIN (1999) Biochemical genetic differentiation of the steppe viper (Vipera ursinii group) in Ukraine and Romania. *Abstracts Tenth Ord. Gen. Meet. S.E.H., Irakleio 1999*, pp. 88–90.

KRAMER, E. (1961) Variation, Sexualdimorphismus, Wachstum und Taxonomie von Vipera ursinii (Bonaparte, 1835) und Vipera kaznakovi Nikolskij, 1909). *Rev. Suisse Zool.* **68**: 627–725.

KRECSÁK, L. & Ş. ZAMFIRESCU (2001): Ecological situation and morphological characteristics of Vipera ursinii moldavica in the "Valea Lui David" natural reserve. *Russian J. Herpetology* **8**(1): 69–73.

LARSON, A. & P. CHIPPINDALE (1993) Molecular approaches to the evolutionary biology of Plethodontid salamanders. *Herpetologica* **49**(2): 204–215.

LATIFI, M. (1985) *The snakes of Iran.* Iran Department of Environment, Tehran. 221 pp. [in Farsi]

LATIFI, M. (1991) *The snakes of Iran.* Soc. Study Amphib. Reptiles, Oxford, Ohio (SSAR Publications, Contributions to Herpetology No. 7, 1–159). [English translation]

LEPRI, G. (1923) Su la presenza della Vipera berus L. Nell Appennino centrale. *Boll. Ist. Zool. Univ. Roma* **1**: 73–78.

LIPTÓI, K., ÚJVÁRI, B., KORSÓS, Z. & A. HIDAS (1999) Investigation of the karyotype of Vipera ursinii rakosiensis. *Állattenyésztés és Takarmányozás* **48**(1): 90–91.

MARX, H. & A. B. RABB (1970) Character analysis: an empirical approach applied to advanced snakes. *J. Zool., London* **161**: 525–548.

MARX, H. & A. B. RABB (1972) Phyletic analysis of fifty characters of advanced snakes. *Fieldiana Zool.* **63**: 1–321.

MCDIARMID, R. W., CAMPBELL, J. A. & T. TOURÉ (1999) *Snake species of the world. A taxonomic and geographic reference.* The Herpetologists' League, Washington, DC. Vol. 1, 511 pp.

MÉHELY, L. (1893) Die Kreuzotter (Vipera berus L.) in Ungarn. *Zool. Anz. Leipzig* **16**: 186–192.

MÉHELY, L. (1894) Vipera ursinii Bonap., eine verkannte Giftschlange Europas. *Zool. Anz. Leipzig* **17**: 57–61, 65–71, 86–87.

MÉHELY, L. (1911) Systematisch-phylogenetische Studien an Viperiden. *Annls hist.-nat. Mus. natn. hung.* **9**: 186–243.

MERTENS, R. (1952*a*) Amphibien und Reptilien aus der Türkei. *Rev. Fac. Sci. Univ. Istanbul. Ser. B.* **17**: 41–75.

MERTENS, R. (1952*b*) Nachtrag zu "Amphibien und Reptilien aus der Türkei". *Rev. Fac. Sci. Univ. Istanbul. Ser. B.* **17**: 353–355.

MERTENS, R. & L. MÜLLER (1928) Liste die Amphibien und Reptilien Europas. *Abh. Senck. naturf. Ges.* **41**(1): 1–62.

MERTENS, R. & H. WERMUTH (1960) *Die Amphibien und Reptilien Europas* (Dritte Liste nach dem Stand vom 1. Januar 1960). Frankfurt am Main (Kramer), 264 pp.

NETTMANN, H.-K., DÜLGE, R., HIELEN, B., RAHMEL, U. & C. SCHNAUDER (1992) Vertical distribution pattern of green lizard species (Lacerta s. str.) in the Pindos Mountain Chain in central Greece. *Proc. Sixth Ord. Gen. Meet. S.E.H., Budapest 1991*, pp. 347–350.

NIKOLSKY, A. M. (1927) Coluber (Vipera) sachalinensis (Tzar.) und seine Geschichte. *Annaire Mus. Zool. Acad. Sci. Urss* **27**: 247–260. [in Russian]

NIKOLSKY, A. M. (1964) *Fauna of Russia and adjacent countries*, Reptiles, Vol. 2. Israel Program for Scientific Translations, Jerusalem, vi+247 p. (Translation of work from 1916).

NILSON, G. (1998) Venomous snakes in west Asia: Applicability of current species concepts. Proc. Asian Herpetological Meeting, Huangshan, Anhui, China, 1992. *Russian Journal of Herpetology* **5**(2): 92–96.

NILSON, G. & C. ANDRÉN (1986) The mountain vipers of the Middle East – The Vipera xanthina complex (Reptilia, Viperidae). *Bonn. zool. Monog.* **20**: 1–90.

NILSON, G. & C. ANDRÉN (1987) Morphological variation and phylogeny of the alpine European and Asiatic Vipera ursinii populations. *Proc. Fourth Ord. Gen. Meet. S.E.H.*, Nijmegen 1987. Fac. Sci. Nijmegen, pp. 293–296.

NILSON, G. & C. ANDRÉN (1988) A new subspecies of the subalpine meadow viper, Vipera ursinii (Bonaparte) (Reptilia, Viperidae), from Greece. *Zoologica Scripta* **17**(3): 311–314.

NILSON, G. & C. ANDRÉN (1989) Reproductive ecology and demography in Vipera. *First World Congress of Herpetology, University of Kent, Canterbury. Abstract.*

NILSON, G. & C. ANDRÉN (1997) Evolution, systematics and biogeography of Palaearctic vipers. *In* THORPE, R. S., WÜSTER, W. & A. MALHOTRA (eds) *Venomous Snakes – Ecology, Evolution and Snakebites. Symp. Zool. Soc., London* **70**: 31–42.

NILSON, G., ANDRÉN, C. & B. FLÄRDH (1988) Die Vipern der Türkei. *Salamandra* **24**(4): 215–247.

NILSON, G., ANDRÉN, C. & B. FLÄRDH (1990) Vipera albizona, a new mountain Viper from central Turkey, with comments on isolating effects of the Anatolian "Diagonal". *Amphibia–Reptilia* **11**: 285–294.

NILSON, G., ANDRÉN, C. & U. JOGER (1993) A reevaluation of the taxonomic status of the Moldavian steppe viper based on immunological investigations, with a discussion of the hypothesis of secondary intergradiation between Vipera ursinii rakosiensis and Vipera (ursinii) renardi. *Amphibia–Reptilia* **14**: 45–57.

NILSON, G., HÖGGREN, M., TUNIYEV, B. S., ORLOV, N. L. & C. ANDRÉN (1994) Phylogeny of the vipers of the Caucasus (Reptilia, Viperidae). *Zoologica Scripta* **23**(4): 353–360.

NILSON, G., TUNIYEV, B. S., ORLOV, N. L., Höggren, M. & C. ANDRÉN (1995) Systematics of the vipers of Caucasus: Polymorphism or sibling species? *Asiatic Herpetological Research* **6**: 1–26.

NILSON, G., TUNIYEV, B. S., ANDRÉN, C., ORLOV, N. L., JOGER, U. & H.-W. HERRMANN (1999*a*) Taxonomic position of the Vipera xanthina complex. *Kaupia* **8**: 99–102.

NILSON, G., TUNIYEV, B. S., ANDRÉN, C. & N. L. ORLOV (1999*b*) Vipers of Caucasus: Taxonomical considerations. *Kaupia* **8**: 103–106.

OBST, F.-J. (1963) Amphibien und Reptilien aus der Mongolei. *Mitt. Zool. Mus. Berlin* **39**(2): 361–370.

OBST, F.-J. (1983) Zur Kenntnis der Schlangengattung Vipera (Reptilia, Serpentes, Viperidae). *Zool. Abh.* **38**(13): 229–235.

ORLOV, N. L. & B. S. TUNIYEV (1986) The recent areas, their possible genesis and the phylogeny of three viper species of Eurosiberian group of the Vipera kaznakowi complex in the Caucasus. *In*

ANANJEVA, N. B. & L. J. BORKIN (eds) *Systematics and Ecology of Amphibians and Reptiles. Proc. Zool. Inst. Leningrad* **157**: 107–135.

ORLOV, N. L. & B. S. TUNIYEV (1990) Three species in the Vipera kaznakowi complex (Eurosibirian group) in the Caucasus: their present distribution, possible genesis, and phylogeny. *Asiatic Herpetological Research* **3**: 1–36.

OSTROVSKIKH, S. V. (1997) Different forms of melanism and its age development in the populations of steppe viper Vipera renardi (Christoph, 1861). *Russian Journal of Herpetology* **4**(2): 186–191.

PARASKIV, K. P. (1956) *Reptiles of Kazakhstan*. Alma-Ata, Acad. Sci. Kazakhstan, S.S.R. 228 pp. [in Russian]

PETERSON, C. R., GIBSON, A. R. & M. E. DORCAS (1993) The causes and consequences of body-temperature variation. Pp. 241–314. *In* SEIGEL, R. A. & J. T. COLLINS (eds) *Snakes – Ecology & Behavior*. McGraw-Hill, Inc.

POZZI, A. (1966) Geonemia e catalogo ragionato degli anfibi e dei rettili della Jugoslavia. *Natura, Milano* **57**: 5–55.

PSENNER, H. (1939) *Die Vipern Grossdeutchlands*. Gustav Wenzel & Sohn, Braunschweig, Berlin, 64 pp.

PUZACHENKO, A. YU., BAKLUSHINSKAYA, I. YU., LYAPUNOVA, E. A., & A. A. VLASOV (1997) Karyotype of Vipera ursini (Reptilia, Viperidae) from Streletskaya Steppe. *Vestnik-Zoologii* **31**(3): 81–82. [in Russian]

REUSS, TH. (1929) Fünf Fotos von Giftschlangen. *Koelner Illustrierte Zeitung* 12.I.1929, No. 2.

REUSS, TH. (1933) "Fortsetzung und Schluss der Originalberichte". *Nachr.-Bl. Aqu.-u. Terr.-Ver., Berlin* **1933**: 372–373.

REUSS, TH. (1935) Erläuterungen zur Typenfrage in der Zoologie an hand von Bildern europäischer Giftschlangen. *Nachr.-Bl. Aqu.-u. Terr.-Ver., Berlin* **16**: 213–218.

RADOVANOVIC, M. (1941) Zur Kenntnis der Herpetofauna des Balkans. *Zool. Anz. Leipzig* **136**: 145–159.

RADOVANOVIC, M. (1964) Die Verbreitung der Amphibien und Reptilien in Jugoslavien. *Senck. biol.* **45**: 553–561.

SAID-ALIEV, S. A. (1979) *Amphibians and reptiles of southern Tadzhikistan*. Acad. Sci. Tadzikistan, S.S.R., Dushanbe, 145 pp. [in Russian]

SAINT GIRONS, H. (1977) Caryotypes et évolution des Vipéres Européenes (Reptilia, Viperidae). *Bull. Soc. Zool. France* **102**: 39–49.

SAINT GIRONS, H. (1978) Morphologie externe comparée et systematique des Vipéres d'Europe (Reptilia, Viperidae). *Rev. Suisse Zool.* **85**: 565–595.

SAINT GIRONS, H. (1980) Biogéographie et évolution des vipéres européennes. *C. R. Soc. Biogéogr.* **496**: 146–172.

SAINT GIRONS, H. (1982) Reproductive cycle of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* **38**: 5–16.

SCHWARZ, E. (1936) Untersuchungen über Systematik und Verbreitung der europäischen und mediterranen Ottern. *Behringwerke-Mitteilungen* **7**: 159–262.

SIGG, H. (1987) Nachforschungen über Vipera ursinii anatolica Eiselt and Baran, 1970 im westlichen Taurus. *Herpetofauna* **9**: 25–34.

SOCHUREK, E. (1984) Liste des Schlangen Jugoslawiens. *Elaphe* **2**: 34–35.

SOULÉ, M. E. (1979) Heterozygosity and developmental stability: another look. *Evolution* **33**(1): 396–401.

STANLEY, S. M. (1992) *Exploring earth and life through time*. Freeman and Co, 538 pp.

STEINHEIL, F. (1927) *Europas Schlangen*.

STENINIGER, F. F. & F. RÖGL (1984) Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys. *In* DIXON, J. E. & A. H. F. ROBERTSON (eds) *The geological evolution of the Mediterranean. Geological Society Special Publ.* **17**: 659–668.

STENINIGER, F. F., RABEDER, G. & F. RÖGL (1985) Land mammal distribution in the Mediterranean Neogene: A consequence of geokinematic and climatic events. Pp. 559–571. *In* STANLEY, D. J. & F.-C. WEZEL (eds) *Geological Evolution of the Mediterranean Basin.*

STRAUCH, A. (1869) Synopsis der Viperiden, nebst Bemerkungen über die geographische Verbreitung dieser Giftschlangen-Familie. *Mém. Acad. imp. Sci. St.-Pétersbourg* **14** (7): 1–144.

STRAUCH, A. (1873) Die Schlangen des Russischen Reiches, in systematischer und zoogeographischer Beziehung. *Mém. Acad. imp. Sci. St.-Pétersbourg* **21**(7): 1–188.

STUMPEL, A., PODLOUCKY, R., CORBETT, K., ANDRÉN, C., BEA, A., NILSON, G. & M. E. OLIVEIRA (1992) Threatened reptiles in Europe requiring special conservation measures. *Proc. Sixth Ord. Gen. Meet. S.E.H., Budapest 1991*, pp. 25–34.

SWOFFORD, D. L. (1989) *PAUP – phylogenetic analysis using parsimony, version 3.0.* Illinois Natural History Survey, Campaign, Illinois.

SZYNDLAR, Z. (1984) Fossil snakes from Poland. *Acta Zool. Cracov.* **28**(1): 1–156.

SZYNDLAR, Z. (1991) A review of Neogene and Quaternary snakes of central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios geol.* **47**: 237–266.

TAKÁCS, Z., KORSÓS, Z. & M. JANISCH (1987) Conservation status of the endangered Vipera ursinii rakosiensis in Hungary. *Proc. Fourth Ord. Gen. Meet. S.E.H.*, Nijmegen 1987. Fac. Sci. Nijmegen, pp. 391–394.

TENYIÉ, A. (1987) Observations Herpétologiques en Turquie, 1ère Partie. *Bull. Soc. Herp. Fr.* **43**: 9–18.

TERENTEV, P. V. & S. A. CHERNOV (1965) *Key to amphibians and reptiles.* Ed. 3. 315 pp. (Translation of work of 1949). Israel Program for Scientific Translations, Jerusalem.

TIEDEMANN, F. (1990) *Lurche und Kriechtiere Wiens.* J and V Edition Wien Verlagsges. m.b.H., pp. 1–200.

TOKTOSUNOV, A. T., MAZIK, E. YU., KASYMALIEVA, E. B. & N. D. IMANALIEVA (1992) Specific characters of the karyotypes of some snake species (Colubridae, Viperidae, Crotalidae) from the Northern Tien Shan. *Zoologicheskii Zhurnal* **71**(5): 118–127. [in Russian with English summary]

TÖRÖK, Z. (1996) The actual state of Vipera ursinii at the "Danube Delta" Biosphere Reserve. Danube Delta Institute, Tulcea, Romania, unpubl. report.

ÚJVÁRI, B., KORSÓS, Z. & KISBENEDEK, T. (1998) A tűz mint veszélyeztető tényező a rákosréti vipera élőhelyén. (Fire hazard in the habitat of the endangered Hungarian meadow viper.) *Természetvédelmi Közlemények* **7**: 151–165.

VANCEA, ST. & V. IONESCU (1954) Contributiuni la Studiul Viperei de Stepa. *Anal. Univ. "Al. I. Cuza" Iasi* **1**(1–2): 241–248.

VANCEA, ST., FUHN, I. E. & M. BORCEA (1980) Vipera de Stepa (Vipera ursinii) si necesitatea ocrotirii ei. *Ocrot. nat. med. inconj. Bucuresti* **24**(1): 49–52.

VANCEA, St., SAINT GIRONS, H., FUHN, I. E. & B. STUGREN (1985) Systématique et répartition de Vipera ursinii (Bonaparte, 1835) (Reptilia, Viperidae), en Roumanie. *Bijdragen tot de Dierkunde* **55**(2): 233–241.

VEDMEDERJA, V. I. (1981) On the subspecies of Vipera ursinii from the USSR steppes. *In* DAREVSKIJ, I. S., ANANEVA, N. B., BARKAGAN, Z. S., BORKIN, L. YA., SOKOLOVA, T. M. & N. N. SHCHERBAK (eds) *The problems of herpetology: abstracts.* Nauka, Leningrad, pp. 29–30. [in Russian]

VEDMEDERJA, V. I., ORLOV, N. L. & B. S. TUNIYEV (1986) On the taxonomy of the three viper species of the Vipera kaznakowi complex. *In* ANANJEVA, N. B. & L. J. BORKIN (eds) *Systematics and Ecology of Amphibians and Reptiles. Proc. Zool. Inst. Leningrad* **157**: 55–61.

VEITH, G. (1991) Die Reptilien Bosniens und der Herzegowina, Teil II. *Herpetozoa* **4**(1–2): 1–96.

VINEGAR, A. (1973) The effects of temperature on the growth and development of embryos of the Indian python, Python molurus (Reptilia: Serpentes: Boidae). *Copeia* **1973**: 171–173.

VOZENILEK, P. (1979) Several notes on the subspecies of Vipera ursinii. *Fauna Bohemiae Septentrionalis, No. 4,* Usti Nad Lebem, pp. 29–46.

WERNER, F. (1895) Die Reptilien und Batrachienfauna der Jonischen Inseln. *Verh. zool.-bot. Ges. Wien* **44**(1894): 225–237.

WERNER, F. (1897) *Die Reptilien und Amphibien Oesterreich-Ungarns und der Occupationsländer.* A. Pichler's Witwe & Sohn, Wien, 160 pp.

WERNER, F. (1920) Zur Kenntnis der Reptilien- und Amphibienfauna Albaniens. *Zool. Anz., Leipzig* **51**: 20–23.

WETTSTEIN, O. V. (1952) Vipera renardi aus Persien. *Zool. Anz., Leipzig* **150**: 266–268.

ZEROVA, G. A. (1992) Vipera (Daboia) ukrainica – a new viper (Serpentes; Viperidae) from the Middle Sarmatian (Upper Miocene) of the Ukraine. *N. Jb. Geol. Paläont. Abh.* **184**(2): 235–249.

ZEROVA, G. A., LUNGU, A. N. & V. M. CKHIKVADZE (1986) Large fossil vipers from the Northern Black Seaside and Transcaucasus. *Proc. Zool. Inst., Leningrad* **158**: 89–99.

ZHAO, E.-M. & K. ADLER (1993) *Herpetology of China.* Soc. Study Amphib. Reptiles, Oxford, Ohio, 522 pp. (SSAR Publications, Contributions to Herpetology No. 10).

ZHAO, E.-M. & Y.-M. JIANG (1979) Preliminary studies on snakes of northern Xinjiang. *Acta Herpetol. Sinica* **2**(1): 1–24.

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FACTOR(S) INFLUENCING MEIOFAUNA AND NEMATODES OF THE SUBMERGED EULITTORAL ZONE OF LAKE SAKADAŠ (NATURE RESERVE KOPAČKI RIT, CROATIA)

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Benthic fauna samples were taken from a sandy submerged eulittoral site at Lake Sakadaš, Kopački rit (Croatia) from November 1997 to December 1998. The meiofauna and freshwater nematode abundance pattern and diversity were analysed with regard to water-level fluctuations and seasonal temperature changes. Meiofauna abundance and diversity showed temporal variations. The nematode relative abundance varied from 4% up to 90% of total meiofauna abundance, although totally absent in August. In total, 26 nematode species were recorded. The composition of nematode species depends on water-level fluctuation. Water levels above 200 cm drasticaly changed the composition of species. *Brevitobrilus stefanskii*, *Tobrilus gracilis* and *Mononchus aquaticus* chewers were the dominant species during the low and the middle water level, and suction feeders were dominant during the high water-level. Temperature and water-level fluctuations determined the diversity and abundance of the benthic fauna in the submerged eulittoral zone of Lake Sakadaš.

Key words: eulittoral, meiofauna, nematode, water-level fluctuation

INTRODUCTION

Meiofauna is a term that refers to the group of small benthic metazoans that pass through a 1 mm or 0.5 mm sieve and are retained by a 0.063 mm sieve (or 0.045 or 0.042 mm) – there is no consensus on the exact limits of the range among scientists (NALEPA & ROBERTSON 1981, HEIP *et al.* 1988, TRAUNSPURGER & DREWS 1996). Eulittoral meiofauna have not been studied much by benthic ecologists, largely due to their small size and the difficulties in studying organisms that live in sediments. Acari, Cladocera, Copepoda, Nematoda, small Oligochaeta, Ostracoda, Rotifera, Tardigrada, small Turbellaria and insect larvae of early instars are included in this group of the benthic community (WASILEWSKA 1973, NALEPA & ROBERTSON 1981). PENNAK (1988) defined the meiofauna as organisms that measure less than 2 mm in total length. Rotifera, Nematoda, Tardigrada, Copepoda and Oligochaeta dominate the interstitial beach meiofauna (PENNAK 1988) while Gastrotricha, Turbellaria, and first instars of insect larvae are less frequent on the sandy beaches. The distribution, diversity, and abundance of the major eulittoral meiofauna groups depend on the temperature, sediment type, amount of organic detritus, oxygen content, food resources and the water-level fluctuation

(MCINTYRE 1969, WASILEWSKA 1973, KAJAK 1988). According to many authors (all in WASILEWSKA 1973 and WHITMAN *et al.* 1994), the interstitial meiofauna is rich and diverse in the aquatic sand.

According to SCHNEIDER (1922), MICOLETZKY (1925), and WASILEWSKA (1973), the most frequent nematodes in the submerged eulittoral of the Holstein lakes, the Danish lakes, and Mikołajskie Lake were the species of the *Tobrilus* genus (some of them transferred to genus *Brevitobrilus*) and the Chromadorinae subfamily. MICOLETZKY (1925) established the species *Tobrilus (Brevitobrilus) stefanskii* as a species strongly associated with the submerged eulittoral sand. WASILEWSKA (1973) found the following species in the submerged part of the eulittoral: *Monhystera paludicola, Tobrilus longus, Aphanolaimus attenuatus, Ironus tenuicaudatus, Chromadorita leukarti, Eumonhystera dispar, Eumonhystera vulgaris, Plectus cirratus*. Some other species were irregularly found in the submerged eulittoral, too: *Monhystera agilis, M. stagnalis, Chromadorina bioculata, Tobrilus gracilis, Tripyla papillata, Alaimus primitivus, Mononchus papillatus, Dorylaimus helveticus* and *D. stagnalis* (all in WASILEWSKA 1973). Furthermore, the species *Monhystera stagnalis* and *Dorylaimus stagnalis* (*D. helveticus*) are the characteristic species in eutrophic lakes and small warm ponds (PREJS 1970).

The nematodes are the most abundant, and the species' richest organism group of meiofauna in the benthos of marine, estuarine and freshwater habitats, and probably play a major role in the nutrient cycle of lacustrine bottoms (SCHIEMER *et al.* 1969, TRAUNSPURGER 1996). They feed on bacteria, fungi, algae, plants, and other organisms. In order to determine their functional role in the sediment, the nematodes were divided into four feeding types according to the shape and the size of their buccal cavity: deposit feeders, epistrate feeders, chewers, and suction feeders (TRAUNSPURGER 1997).

The objective of this study was to establish the spatial and temporal patterns in meiofauna and nematode fauna abundance and the diversity in the submerged eulittoral site with regard to the seasonal temperature variation and the water-level fluctuation connected to the water-level fluctuation of the Danube.

MATERIALS AND METHODS

Lake Sakadaš, oval in shape with relatively steep shore slopes, is the deepest water depression (with an average depth of 7 m) in the Kopački rit flooded area, in the narrow belt between two rivers, the Drava and the Danube, in the northeastern part of Croatia (Fig. 1). The total surface of Lake Sakadaš is difficult to measure because the surface changes considerably with the water-level fluctuation, but the estimated average surface amounts up to 6 ha (MIKUSKA, pers. com.). The water-level fluctuation of Lake Sakadaš is determined by the water-level fluctuation of the Danube and to a lesser extent influenced by the water-level fluctuations of the Drava, amount of precipitation or changes of

groundwater-level. A long-term investigation established that Lake Sakadaš is a eutrophic lake (MIHALJEVIĆ & NOVOSELIĆ 2001).

The representative submerged part of the eulittoral sandy site was chosen along the straight shoreline of Lake Sakadaš because of the constant changes of shoreline due to the water-level fluctuation and the accumulation of organic matter from the land overgrown with *Salix* spp and *Populus* spp.

Sediment samples were collected monthly, from November 1997 to December 1998, 15 cm below the water-level. For meiofauna analysis, at each sampling period six sediment samples were taken from the 0–10 cm sediment layer with a metal hand corer of 5 cm in diameter.

The sediment samples used for meiofauna anaysis were fixed in 10% neutralised (4% formaldehyde) and rose bengal stained formalin. The fauna was extracted by the elutriation method (UHLIG *et al.* 1973). The sediment was sieved through a 60 μm mesh. The nematodes were picked out for species identification and permanent slides were prepared according to SEINHORST's (1953) method.

Fourteen additional core samples were taken for bacterial analysis pursuant to KUZNECOV and DUBININA (1989). The standard indirect microbiological method includes the following analysis: the number of eutrophic bacteria (CFU-e), oligotrophic bacteria (CFU-o), and aerobe sporogenic bacteria.

Furthermore, in December 1997, January, February, April, August and November 1998, sediment samples were collected for granulometric analysis. The sediment samples were processed by a combined method (by courtesy of Neda Vdović, Ruđer Bošković Institute, Zagreb): fraction seaving ≥ 32 μm through a standard mesh (Fritsch, Germany) and by fraction analyses ≤ 32 μm using the coulter counter (Coulter Counter, TA II, Coulter Electronics Ltd., England). The sediment classification was performed according to SHEPARD (1932).

At the same time, the water temperature was recorded. For the evaluation of the site studies with regard to the organic enrichment, water samples were taken for the analysis of dissolved oxygen, COD (chemical oxygen demand), NH_4-N, NO_2-N and NO_3-N analysis. The dissolved oxygen was de-

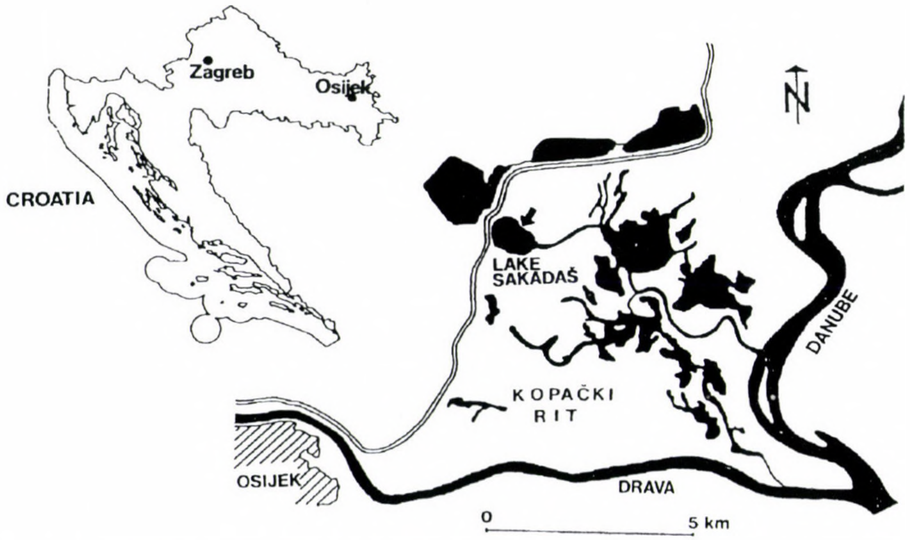


Fig. 1. The study area in the Kopački rit Nature Reserve, Croatia, at the Lake Sakadaš submerged eulittoral section

termined by the WINKLER method (APHA 1985). COD (chemical oxygen demand), NH_4-N, NO_2-N, and NO_3-N analysis were carried out following the APHA (1985).

The Croatian Water Resource Management Osijek (Croatian Waters Zagreb) supplied the water-level fluctuation data.

The abundance was expressed as the number of individuals per 75.36 cm^2. Dominance (D%), as a population parameter, was calculated for the meiofauna and nematodes in respect to time variability (ODUM 1971).

ANOVA and LSR tests (PARKER 1975) were used for statistical anaysis, to quantify the differences in meiofauna and nematode abundance depending on seasonal and monthly differences in the Lake Sakadaš water-level. In this study, the sampling months were divided into three groups according to different water-levels: the first one included the months with water-levels ranging from –14 cm to 100 cm (November 1997, February and August 1998); the second group included the months with a water-level ranging from 100 to 200 cm (December 1997, January, March, June and July 1998); and the third group included months with water-levels above 200 cm (September and December 1998).

Univariate and multivariate statistical methods were used to determine factor(s) influencing the temporal and spatial variations in meiofauna and nematode associations. Univariate statistical methods were used to determine the stress levels. The number of species was counted, the SHANNON-WIENER Index of diversity (H'), MARGALEF's diversity index (MARGALEF 1951, SHANNON & WIENER 1963), as well as PIELOU's evenness (J), were calculated (ODUM 1971). In order to link the environmental factors with the sediment fauna, multivariate statistical methods, including principal factor analysis (CLARKE & WARWICK 1990), were conducted.

The nematodes encountered during the study were divided into four feeding groups according to TRAUNSPURGER (1997).

RESULTS

The physicochemical parameters were analysed in order to characterize the studied site (Fig. 2, Table 1). During the investigated period, minimum water tem-

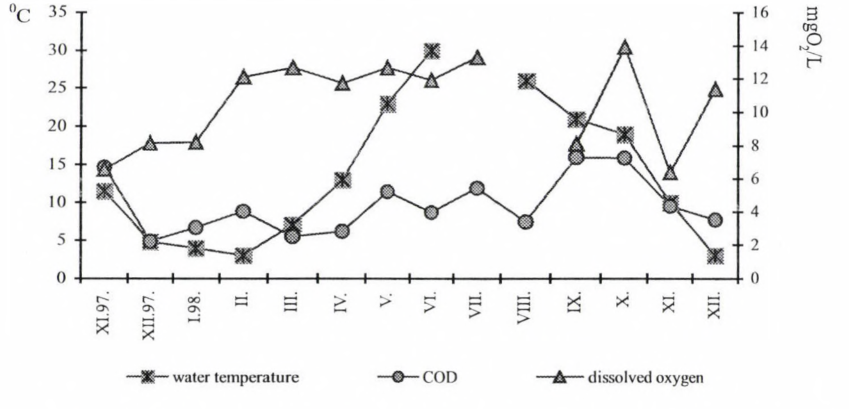


Fig. 2. Physicochemical water parameters at Lake Sakadaš during the investigation period

Table 1. Chemical water parameters from the Lake Sakadaš submerged eulittoral site

	November 1997	December 1997	January 1998	May 1998
NH_4-N (mg N/L)	1.393	1.410	0.488	0.465
NO_3-N (mgN/L)	1.587	0.767	0.933	0.837
NO_2-N (mgN/L)	0.011	0.022	0.001	0.008

perature was recorded in February and December 1998 (3 °C), and maximum temperature was recorded in June (30 °C). Dissolved oxygen ranged from 6.39 mg/L (November 1998) to 13.92 mg/L (October 1998). COD (chemical oxygen demand) showed three high values during the investigated period. The first one was recorded in November 1997 (14.63 mg O_2/L), the second one in September (15.95 mg O_2/L), and the third one in October 1998 (15.89 mg O_2/L). Additionally, high NH_4-N and NO_2-N values were recorded for the first two months of the investigation, while NO_3-N values were highest in November 1997.

The lowest water-levels (Fig. 3) were recorded in November 1997 (–14 cm), February (26.07 cm), and August 1998 (74.03 cm). At the beginning of October 1998, the water-level started to increase, so that in November 1998 the highest water-level was recorded (442.93 cm), moving the sampling place 30 m inland. Due to the water-level fluctuation of Lake Sakadaš, the border of the lake moved the sampling place, so it was located between the trees surrounding the lake.

In general, the sediment in the study site is sand, with a very low percentage of silt and clay (Table 2).

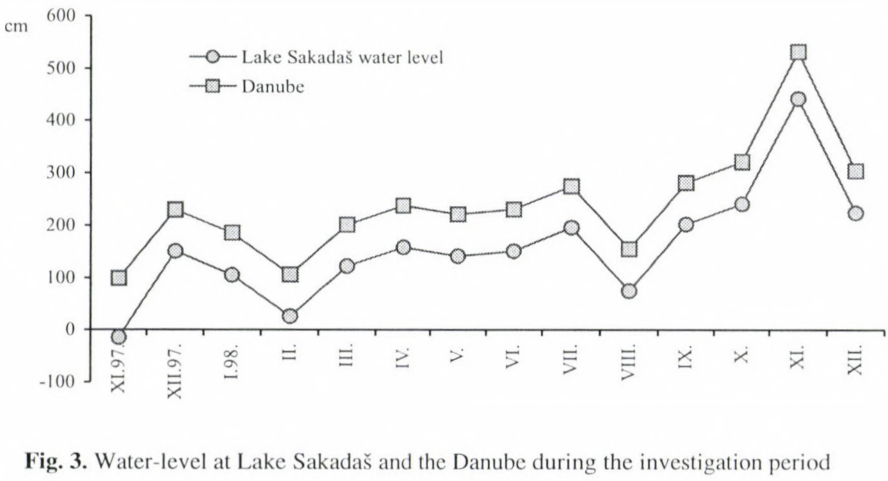


Fig. 3. Water-level at Lake Sakadaš and the Danube during the investigation period

Considerable variations in the number of eutrophic (psihrophils and mesophils), oligotrophic, and aerobe sporogenic bacteria were recorded (Fig. 4).

A negative correlation was recorded for the total number of bacteria and the water temperature ($r=-0.601$, $df=11$, $p<0.05$).

In the sediment samples, 11 meiofaunal taxa were recorded: Nematoda, Copepoda, Oligochaeta, Gastrotricha, Cladocera, Tardigrada, early instar of insect larvae, Turbellaria, Rotifera, Crustacean larvae and Hydroacarina. Maximum meiofauna abundance was recorded in April (1454 ind./75.36 cm^2) and the minimum in August (10 ind./75.36 cm^2). Significant differences in total meiofauna abundance were recorded, discriminating April and August samples at $p=0.05$. Furthermore, ANOVA and LSR tests of significance showed no differences in meiofauna abundance between the middle and the high water-level and between the high and the low water-levels. However, significant differences in meiofauna abundance were recorded between the middle and the low water-levels ($F=57.272$; $df=2,81$; $p<0.01$). The greatest numbers of meiofaunal taxa were recorded in February (eight), October (nine), and December (eight) of 1998, while the lowest number (three) was recorded in August.

The meiofauna was dominated by nematodes in most of the months, except for August (totally absent), October, November and December 1998. The nematodes form 4% to 98.3% of the total meiofauna population. The copepods dominated in August by 50% of the total meiofauna population, followed by Rotifera (40%). Rotifera was the second in dominance in the February sample, by 23.3%. Oligochaeta dominated in the December 1998 sample, by 55.3% of the total meiofauna population, and was subdominant in November 1997 by 18.7%.

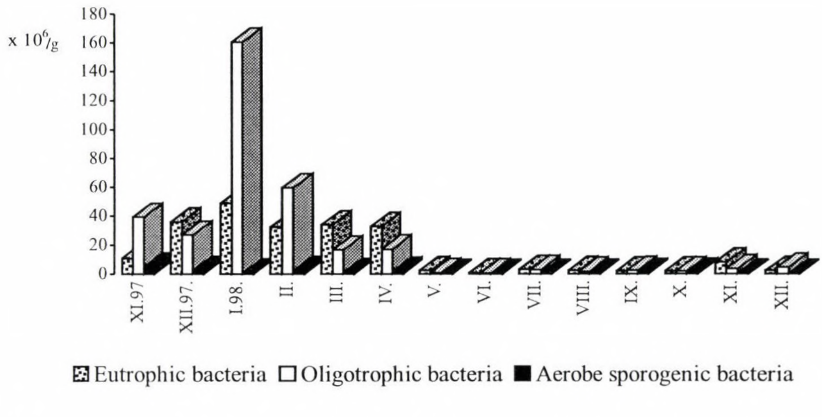


Fig. 4. Total number of bacteria in submerged eulittoral sediment during the investigation period

Table 2. Sediment-bound particle size analysis at the investigated site of Lake Sakadaš

Particle size	December 1997	January 1998	February 1998	April 1998	August 1998	November 1998
% sand	94.5	95.04	95.04	93.70	94.98	98.57
% silt	4.5	4.7	4.7	6.05	4.88	1.28
% clay	1.0	0.26	0.26	0.25	0.14	0.15

Gastrotricha was subdominant in the June sample by 26.5% of the total meiofauna population. Cladocera dominated in November 1998, by 58.3% of total meiofauna abundance. The highest Cladocera abundance occurred during the high water-level period (>200 cm), and a positive significant correlation was recorded between the water-level fluctuation and Cladocera abundance ($r=0.729$, $n=14$, $p<0.01$). ANOVA and LSR tests of significance showed significant differences in the meiofauna abundance between the winter-spring (high abundance) and summer-autumn period with lower abundance ($F=21.105$; $df=3,80$; $p<0.01$).

Altogether, 26 nematode species were identified in the sandy site during the investigated period. The most frequent species were *Mononchus aquaticus, Brevitobrilus stefanskii*, and *Dorylaimus stagnalis*. The abundance of *Brevitobrilus stefanskii* increased from the autumn to the winter period, and started to decrease thereafter ($F=19.100$; $df=3,56$; $p<0.01$). A significant negative correlation between the abundance of *Brevitobrilus stefanskii* and COD ($r=-0.576$, $df=12$; $p=0.05$), as well as a significant positive correlation for that species and the total bacteria number, were recorded.

Mononchus aquaticus was present throughout the year, but the mean abundance reached its maximum in April and July, dominating by 66% and 74%, respectively, with regard to the total nematode abundance. The abundance of that species was significantly higher in spring and early summer, and a decrease started with lower water temperature ($F=5.636$; $df=3,56$; $p<0.01$). A significant positive correlation was recorded between the abundance of the two most frequent species, *Brevitobrilus stefanskii* and *Mononchus aquaticus* ($r=0.639$, $df=12$, $p=0.02$). These species were not recorded in the October, November, and December 1998 samples.

Tobrilus gracilis was represented by a lower abundance, except for May and June 1998.

During the investigated period, the species *Brevitobrilus stefanskii, Mononchus aquaticus*, *Tobrilus gracilis*, and *Dorylaimus stagnalis* were recorded almost in all months. ANOVA and LSR tests of significance showed significant differences in the abundance of these species during the period of investigation ($F=8.850$; $df=3,44$; $p<0.01$). The difference between the abundance of species

Brevitobrilus stefanskii and *Mononchus aquaticus* was not significant, as well as between the abundance of *Mononchus aquaticus* and *Tobrilus gracilis*, and between the abundance of *Tobrilus gracilis* and *Dorylaimus stagnalis*. Significant differences in abundance between *Brevitobrilus stefanskii* and *Tobrilus gracilis* with *Dorylaimus stagnalis* were recorded.

A connection between the composition of nematode species and water-level fluctuation was observed by the separation of nematodes into three groups, according to the water-level fluctuation (Table 3). ANOVA and LSR tests of significance discriminate the species composition in the water-level above 200 cm ($F=3.595$; $df=2,39$; $p=0.05$). The factorial analysis based on the nematode species' abundance during the investigated period indicates that two abiotic factors influence the nematode population in the submerged part of eulittoral, while the temperature and water-level fluctuation discriminate the nematode population recorded at the high water-level (Fig. 5). Furthermore, ANOVA and LSR tests of significance discriminate the highest abundance of *Mononchus aquaticus* during the water-levels between 100 and 200 cm (middle water-level) at $p<0.01$. The abundance of *Brevitobrilus stefanskii* was not different between the mid- and low water-levels, but ANOVA and LSR tests of significance ($p<0.01$) discriminate the lowest abundance during the high water-level (above 200 cm).

A factorial analysis for the composition of nematode species discriminates the species that were recorded only at a high water-level, followed by the species

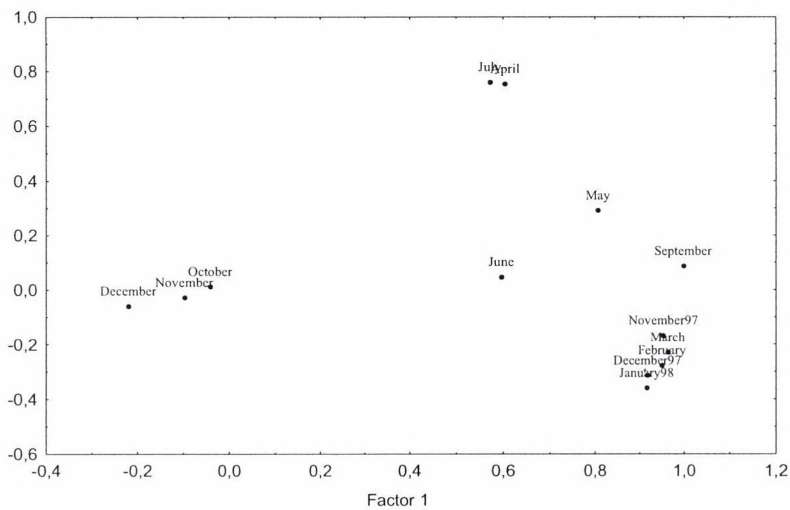


Fig. 5. Factorial analysis based on the nematode species' abundance recorded at the eulittoral sediment submerged section, from November 1997 to December 1998

common for the middle and the high water-level, and finally with species common for the middle and the low water-level (Fig. 6).

The univariate measure (H', d, S, and J) changed over the period of investigation (Fig. 7). Comparing MARGALEF's diversity index in nematode species' abun-

Table 3. Water-level fluctuation (cm) and nematode population (I. water level ranged from –14 to 100 cm; II. water level ranged from 100 to 200 cm; III. water level above 200 cm); FT – feeding type: DF – deposit feeders, EF – epistrate feeders, CH – chewers, SC – suction feeders; % – nematode relative abundance

Nematodes	FT	I.	%	II.	%	III.	%
Monhystera stagnalis	DF	5	3.3	8	0.5	0	0
Brevitobrilus stefanskii	CH	95	62.1	536	32.7	28	28.9
Mononchus aquaticus	CH	22	14.4	859	52.6	16	16.5
Plectus sp. 1	DF	6	3.9	0	0	0	0
Ethmolaimus pratensis	EF	3	1.9	43	2.6	0	0
Dorylaimus stagnalis	SF	5	3.3	40	2.5	3	3.1
Eumonhystera filiformis	DF	4	2.6	60	3.7	0	0
Tobrilus gracilis	CH	9	5.9	44	2.7	10	10.3
Diplogaster rivalis	CH	4	2.6	1	0.1	0	0
Plectus communis	DF	0	0	1	0.1	0	0
Eudorylaimus sp.	SF	0	0	1	0.1	0	0
Prodorylaimus sp. 1	SF	0	0	6	0.4	2	2.1
Tripyla papillata	CH	0	0	3	0.2	0	0
Eumonhystera sp. 1	DF	0	0	1	0.1	7	7.2
Paramononchus sp.	CH	0	0	24	1.5	2	2.1
Thornia sp. 1	SF	0	0	2	0.1	1	1.0
Prodorylaimus sp. 2	SF	0	0	4	0.2	0	0
Dorylaimus sp.	SF	0	0	1	0.1	0	0
Thornia sp. 2	SF	0	0	0	0	7	7.2
Mesodorylaimus sp.	SF	0	0	0	0	2	2.1
Mesodorylaimus bastiani	SF	0	0	0	0	1	1.0
Plectus sp. 2	DF	0	0	0	0	1	1.0
Tobrilus sp.	CH	0	0	0	0	3	3.1
Indent 10	SF	0	0	0	0	10	10.3
Plectus sp. 3	DF	0	0	0	0	1	1.0
Indent 3	SF	0	0	0	0	3	3.1
N		153	100	1634	100	97	100
S		9		17		16	

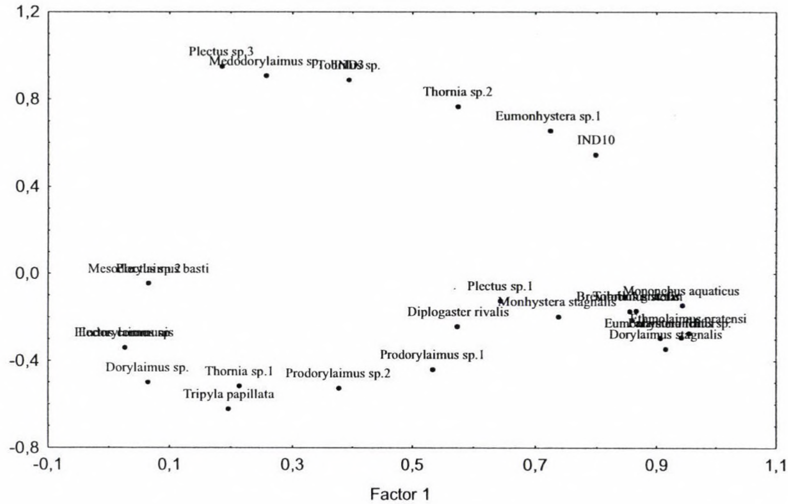


Fig. 6. Factorial analysis based on the composition of nematode species recorded at the eulittoral sediment submerged section, from November 1997 to December 1998

dance between the low, middle, and the high water-level, the ANOVA and LSR tests of significance discriminate the abundance of species at the middle water-level as the lowest (F=23.015; df=2,65; p<0.01). A significant negative correlation was recorded between MARGALEF's diversity index and the water temperature (r=–0.561; n=13; p<0.05). ANOVA and LSR tests of significance showed no

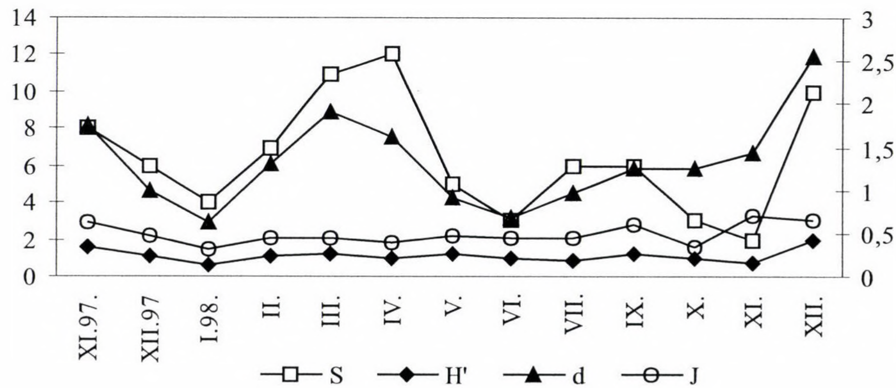


Fig. 7. Nematode population parameters such as number of species (S), SHANNON-WIENER diversity index (H'), MARGALEF's d and PIELOU's J during the investigated period

differences in the number of species between the low and the middle water-level and between the middle and the high water-level. But significant differences in the number of species ($F=75.854$; $df=2,65$; $p<0.01$) were recorded between the low and the high water-level.

According to the shape and size of the buccal cavity, nematodes are divided into four feeding types (Table 3). During the low and the middle water-level, chewers dominated from 72% to 100% of total nematode abundance. An increasing water-level, above 200 cm, changes the feeding-type patterns, so suction feeders dominated from 50% to 80% of total nematodes.

DISCUSSION

The aim of this investigation was to define a temporal pattern of meiofauna and nematode fauna abundance and diversity with regard to water-level fluctuation and water temperature.

During the period of investigation, from November 1997 to December 1998, an irregular water-level of Lake Sakadaš was recorded due to the water-level fluctuation of the Danube. According to the previous investigation, the Danube floods the low ground of Kopački rit to +300 cm of the water-level (MIKUSKA 1979). According to WASILEWSKA (1973), the investigated site at Lake Sakadaš can be determined as eulittoral, which means a "transitional zone between the lake and the surrounding land that covers the area between the maximum and the minimum water-level."

According to CLASEN (1979), NH_4-N and NO_3-N values at the study site exceed the standard values (≤ 0.3 mg/L, ≤ 0.1 mg/L, respectively) and indicate some deterioration in the water-quality due to accumulated organic matter along the borderline between the water and the land.

The dissolved oxygen never dropped below the critical value (6 mg/L), allowing us to exclude organic pollution at the site studied (ZULLINI 1976).

The number of sediment bacteria (eutrophic, oligotrophic, and aerobe sporogenic bacteria) showed a clear temporal variation. A significant increase in eutrophic bacteria from November 1997 to January 1998 occurred. Later a decrease in the number of eutrophic bacteria and an increase in the number of oligotrophic and aerobe sporogenic bacteria indicated a slower mineralization process (ROMANENKO 1985).

In the submerged part of the eulittoral, tidal freshwater marsh, and on sandy beaches a variable number of meiofauna groups was recorded, from four (SCHIEMER *et al.* 1969) to eight and ten, respectively (WASILEWSKA 1973, FENCHEL

1975, WHITMAN *et al.* 1994, YOZZO & SMITH 1995). During the period of investigation of the submerged eulittoral at Lake Sakadaš, the meiofauna was represented by eleven groups, including Nematoda, Copepoda, Oligochaeta, Gastrotricha, Cladocera, Tardigrada, early instars of insect larvae, Turbellaria, Rotifera, Crustacean larvae and Acarina. PENNAK (1988) stated that the dominant freshwater beach interstitial meiofauna includes Nematoda, Rotifera, Tardigrada, Copepoda, and Oligochaeta. Our findings in the present study are consistent with respect to Nematoda, Copepoda, Oligochaeta and Rotifera, but Tardigrada was less frequent in the submerged part of the Lake Sakadaš eulittoral. Gastrotricha, Turbellaria, and early instars of insect larvae in the submerged part of the Lake Sakadaš eulittoral occurred less frequently, as PENNAK (1988) stated for the beaches. Acari was recorded only in November 1998 during the highest water-level, as well as Cladocera was recorded in a high number during the months with a high water-level (above 200 cm). WHITMAN *et al.* (1994) collected water mites incidentally in their study. YOZZO and SMITH (1995) also occasionaly collected Rotifera, Turbellaria, water mites, Chironomida larvae and Cladocera.

We did not observe a clear temporal pattern in the meiofaunal communities. However, maximal meiofauna abundance was recorded for April and minimal for August. But YOZZO and SMITH (1995) recorded minimal meiofauna abundance in April and maximal one in September. SCHIEMER *et al.* (1969) recorded maximum meiofauna abundance (nematodes, tardigrades, and oligochaetes) during springtime (May and June). WASILEWSKA (1973) recorded a maximum meiofauna abundance in June and July. MCINTYRE (1969) mentioned that temperature is the main abiotic parameter that has influenced meiofauna abundance and diversity in the sand beaches exposed to the extreme values of these abiotic parameters. WASILEWSKA (1973) claimed that periodic flooding and drying-up, due to the water-level fluctuation, had exerted an influence on meiofauna abundance and diversity. We found the same pattern for meiofauna abundance and diversity with regard to the submerged part of the eulittoral sediment of Lake Sakadaš.

Nematoda dominated the submerged eulittoral meiofauna except in August (nematoda not recorded) and during the extremly high water-level (October, November, and December 1998), when it was dominated by Rotatoria and Oligochaeta. The nematodes represented 4% of the total meiofauna and reached their maximum dominance in April, amounting up to 98% of the total meiofauna abundance. The data recorded for the Lake Sakadaš eulittoral zone are consistent with the previous findings (PREJS 1970, FENCHEL 1975, WHITMAN *et al.* 1994, YOZZO & SMITH 1995, TRAUNSPURGER 1996). The nematode abundance recorded for the submerged eulittoral was lower than the one recorded for Mikołajskie Lake (WASILEWSKA 1973), the tundra pond (FENCHEL 1975), the one recorded for the

shallow littoral (0.5 m) in the eutrophic Mikołajskie Lake (PREJS 1970, 1977*a*), as well as the one recorded for the oligotrophic Königssee (TRAUNSPURGER 1996). The nematodes manifested a maximum in April, but they were absent in August. Our findings are consistent with that of SCHIEMER *et al.* (1969), who recorded a maximum nematode abundance during springtime. PREJS (1970) recorded a summer decrease in the number of nematodes in the majority of the investigated sites, as well as FENCHEL (1975), who also recorded a decrease in nematode abundance from July to August in a small tundra pond. The absence of nematodes in August could be explained by an extremely high temperature during July and August. According to MCINTYRE (1969) the nematodes move down to a deeper layer under such conditions. An extremely low nematode abundance, recorded in the October, November, and December 1998 samples, was evident due to a high water-level, which flooded the surrounding soil, so that the sampling site moved about 30 m landwards, as WASILEWSKA (1973) recorded for the eulittoral sediment of Mikołajskie Lake.

In total, 26 nematode species were recorded during the period of investigation. That number of species is lower than the one recorded for the submerged eulittoral and shallow sites in Mikołajskie Lake, and the Königssee (PREJS 1970, 1977*a*, TRAUNSPURGER 1996). A higher number of nematode species was recorded than in St. Mortiz Lake (BORNER 1921/1922), in the submerged part of Mikołajskie Lake (WASILEWSKA 1973), and the oligotrophic Char Lake (PREJS 1977*a*). Great variations in nematode species composition were recorded between water-levels. According to WASILEWSKA (1973), great changes in the number of nematode species and the composition of nematodes could be observed due to water-level fluctuations, as we have recorded for the composition of nematode species and abundance at the submerged part of Lake Sakadaš.

Brevitobrilus stefanskii and *Mononchus aquaticus* represented up to 79% of all nematode individuals found except during May and June, when *Tobrilus gracilis* exceeded the number of *Mononchus aquaticus*. The dominance of the genus *Tobrilus* for the submerged eulittoral, as well as for the shallow littoral, is well documented. PREJS (1970) recorded the clear dominance of the *Tobrilus* genus in the gravel with a sand bottom at the shallow littoral. WASILEWSKA (1973) recorded a partial dominance of *Tobrilus longus* and *Brevitobrilus stefanskii*. Less frequent were the species of *Tobrilus gracilis* and *Dorylaimus helveticus*. The compared data indicate the presence of four genera (*Tobrilus, Mononchus, Tripyla* and *Dorylaimus*) and the Chromadorinae subfamily at the submerged eulittoral site. In our investigation, only one species belongs to Chromadoridae, and that is *Ethmolaimus pratensis*. A clear dominance of Chromadoridae for Mikołajskie Lake was recorded by WASILEWSKA (1973) and PREJS (1970), for Char Lake by PREJS

(1977*a*), and for the Holstein and Danish Lakes by SCHNEIDER (1922) and MICOLETZKY (1925). The dominance of nematode species *Brevitobrilus stefanskii* in the sand sediment of the submerged part of eulittoral of Lake Sakadaš confirmed MICOLETZKY's (1925) statement that the species is strongly associated with this type of habitat. Furthermore, in the deepest part of Lake Sakadaš, the species *Brevitobrilus stefanskii* represented only 2% of total nematofauna population. The dominant species in the deepest part of the Lake Sakadaš was *Tobrilus gracilis*, by 76% of the total nematofauna population (VIDAKOVIĆ unpubl. data).

MASTRANTUONO (1993) proposed the range of values of SHANNON and PIELOU indices for a trophic classification. According to the proposed values for the SHANNON index (<2.5) and for the PIELOU index (<0.50), all sampling sites were eutrophic, except in November 1997, September, and December 1998 for the PIELOU index.

Following TRAUNSPURGER's (1997) classification, the submerged eulittoral sandy site of Lake Sakadaš was dominated by chewer nematodes during the low and the middle water-level, which is in concordance with the previous findings for Mikołajskie Lake and the Königssee (PREJS 1970, TRAUNSPURGER 1996). Some changes were observed in nematode feeding types, due to the increase in the water-level above 200 cm. Suction feeders became dominant during the high water-level indicating feeding types connected with the root region, as recorded by PREJS (1977*b*). Significant correlation between *Brevitobrilus stefanskii* abundance and eutrophic bacteria could point out that these species might be deposit feeders (feeding on bacteria and fungi associated with detritus particles). Still, no cuticular remnants of prey were found in the gut. Microscopic observations have shown that these species have detritus particles in the buccal cavity. For that reason, the species of the genus *Tobrilus* might be transferred into deposit feeders.

*

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REFERENCES

APHA (1985) *Standard Methods for the Examination of Water and Wastewater.* Apha, Washington, D. C. 16th ed., 1481 pp.

BORNER, L. (1921–1922) Die Bodenfauna des St. Moritzer Sees. Eine monographische Studie. *Arch. Hydrobiol.* **13**: 1–91, 209–281.

CLARKE, K. R. & WARWICK, R. M. (1990) *Lecture notes prepared for the training on the statistical treatment and interpretation of marine community data.* FAO/IOC/UNEP, Split.

CLASEN, J. (1979) *Regional project shallow lakes and reservoirs. Final report.* OECD Programme for Monitoring of Inland Waters, Paris. 2 Vols.

FENCHEL, T. (1975) The quantitative importance of the benthic microfauna of an arctic tundra pond. *Hydrobiologia* **46**: 445–464.

HEIP, C., WARWICK, R. M., CARR, M. R., HERMAN, P. M. J., HUYS, R., SMOL, N. & VAN HOLSBEKE, K. (1988) Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesndfjord. *Mar. Ecol. Prog. Ser.* **45**: 171–180.

KAJAK, Z. (1988) Considerations on benthos abundance in freshwaters, its factors and mechanisms. *Int. Revue Ges. Hydrobiol.* **73**: 5–19.

KUZNECOV, S. I. & DUBININA, G. A. (1989) *Methods of investigations of aqueous microorganisms.* Nauka. Moskva. 287 pp. [in Russian]

MARGALEF, R. (1951) Diversidad de especies en las comunidades naturales. *Pub. Inst. Biol. app.* **9**: 5–27.

MASTRANTUONO, L. (1993) Zoobenthos associated with submerged macrophytes and evaluation of trophic status in lakes. *Verh. Internat. Verein. Limnol.* **25**: 780–783.

MCINTYRE, A. D. (1969) Ecology of marine meiobenthos. *Biol. Rev.* **44**: 245–290.

MICOLETZKY, H. (1925) Die Freilebenden Süsswasser und Moornematoden Danemarks. *Mem. Acad. Roy. Danemark. Sect. Soc.* **8**: 1–310.

MIHALJEVIĆ, M. & NOVOSELIĆ, D. (2001) Trophic state of the Lake Sakadaš (Nature Reserve Kopački rit, Croatia) in the late autumnal and winter period of 1997/98. *Periodicum Biologorum* **102** (3): 253–257.

MIKUSKA, J. (1979) *Ekološke osobine i zaštita specijalnog zoološkog rezervata "Kopački rit" s posebnim osvrtom na ekologiju kralježnjaka.* Disertacija. Zagreb. 271 pp.

NALEPA, T. F. & ROBERTSON, A. (1981) Screen mesh size affects estimates of macro- and meiobenthos abundance and biomass in the Great Lakes. *Can. Fish. Aquat. Sci.* **38**: 1027–1034.

ODUM, E. P. (1971) *Fundamentals of ecology.* W. B. Saunders Company. Phyladelphia. 574 pp.

PARKER, R. E. (1975) *Introductory statistics for biology.* Studies in biology no. 43. 2nd ed., Edward Arnold Ltd. London. 122 pp.

PENNAK, R. W. (1988) Ecology of freshwater meiofauna. Pp. 39–60. *In* HIGGINS, R. P. & THIEL, H. (eds) *Introduction to the study of meiofauna.* Smithsonian Institution Press, Washington, D.C.

PREJS, K. (1970) Some problems of the ecology of benthic nematodes (Nematoda) of Mikołajskie Lake. *Ekol. Pol.* **9**: 225–242.

PREJS, K. (1977*a*) The littoral and profundal benthic nematodes of lakes with different trophy. *Ekol. Pol.* **25**: 21–30.

PREJS, K. (1977*b*) The nematodes of the root region of aquatic macrophytes, with special consideration of nematode groupings penetrating the tissues of roots and rhizomes. *Ekol. Pol.* **25**: 5–20.

ROMANENKO, V. J. (1985) *Mikrobiologičeskie procesi produkcii i destrukcii organičeskogo veščestva vo vnutrenih vodemah.* Nauka. Lenjingrad. [in Russian]

SCHIEMER, F., LOFFLER, H. & DOLLFFUS, H. (1969) The benthic communities of Neusiedlersee (Austria). *Verh. Internat. Verein. Limnol.* **17**: 201–208.

SCHNEIDER, W. (1922) Freilebende Süsswassernematoden aus ostholsteinischen Seen. *Arch. Hydrobiologia* **13**: 696–735.

SEINHORST, J. W. (1953) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* **4**: 67.

SHANNON, C. E. & WIENER, W. (1963) *The mathematical theory of communication.* Univ. Illinois Press. Urbana. 117 pp.

SHEPARD, F. P. (1932) Sediments of the continental shelves. *Bull. Geol. Soc. Am.* **43**: 1017–1040.

TRAUNSPURGER, W. (1996) Distribution of benthic nematodes in the littoral of the oligotrophic lake (Königssee, National Park Berchtesgaden, FRG). *Arch. Hydrobiol.* **135**: 393–412.

TRAUNSPURGER, W. (1997) Bathymetric, seasonal and vertical distribution of feedingtypes of nematodes in an oligotrophic lake. *Vie Milieu* **47**(1): 1–7.

TRAUNSPURGER, W. & DREWS, C. (1996) Toxicity analysis of freshwater and marine sediments with meio- and macrobenthic organisms: a review. *Hydrobiologia* **328**: 215–261.

UHLIG, G., THIEL, H. & GRAY, J. S. (1973) The quantitative separation of meiofauna. A comparison methods. *Helgoländer wiss. Meeresunters.* **25**:173–195.

WASILEWSKA, B. E. (1973) Microfauna of few eulittoral habitats of Mikołajskie Lake with special consideration to the nematodes (Nematoda). *Ekol. Pol.* **4**: 57–72.

WHITMAN, R. L., ANDRZEJEWSKI, C., KENNEDY, K. J. & SOBAT, T. A. (1994) Composition, spatial-temporal distribution and environmental factors influencing the interstitial beach meiofauna of southern Lake Michingan. *Verh. Internat. Verein. Limnol.* **25**: 1389–1397.

YOZZO, D. J. & SMITH, D. E. (1995) Seasonality, abundance, and microhabitat distribution of meiofauna from a Chickahominy River, Virginia tidal freshwater marsh. *Hydrobiologia* **310**: 197–206.

ZULLINI, A. (1976) Nematodes as indicators of river pollution. *Nematol. Medit.* **4**: 13–22.

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ON THE LEGUMINOUS HOST PLANTS OF SEED PREDATOR WEEVILS (COLEOPTERA: APIONIDAE, CURCULIONIDAE) IN HUNGARY

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Fruit bearing shoots of 139 leguminous species (cca 86% of known species of Leguminosae in Hungary) were collected at 148 sites all over the country since 1978. Only 54 species (38.8%) were found to host altogether 43 weevil species. The rearing method largely reduced the probability of getting adult weevils that may have used a plant only as an adult food source or only as refuge. This strongly increased the reliability of the host plant data obtained. The host plant range showed great differences within and between weevil genera. From the 54 plant species found as hosts, 29 and 11 (altogether 74.1%) harboured only one and two weevil species, respectively. The resource exploitation rate turned out very low at the plant species level.

Key words: Apionini, Tychiini, Leguminosae, specialisation, resource use

INTRODUCTION

In the course of research programmes aiming to reveal the seed predator insects associated especially with wild leguminous species of the Hungarian flora, species of Apionidae and Curculionidae were reared from fruits collected all over the country. This enabled us to get reliable data on the host plant affiliations of weevils. As COLONNELLI and OSELLA (1998) pointed out, the literature contains data on genuine host species on which larval development takes place as well as data on refuge plants which are used only as food, as shelter, and for transport by the adults. Consequently, the reliability of earlier host plant data is often questionable. A further factor of uncertainty is the frequent change in the taxonomy of weevil species. Therefore, below we refer only to recent literature data that support our findings. We deliberately do not mention reports on host plants that differ from ours, because we do not want to repeat possibly dubious data already published.

In the following we discuss the main characteristics of the host plant ranges comparing the data within and between weevil genera taking into consideration also the higher taxa (tribes) of the family of Leguminosae.

METHOD

Short shoots bearing ripe or almost ripe pods or flower heads, in a few instances only pods, were collected throughout Hungary since 1978. Sampling was focused mostly on wild legume species of natural or semi-natural habitats. Cultivated legume species were sampled only occasionally. The samples were put separately in paper bags and were transferred in the laboratory into glass jars covered with linen. The repeated handling of the plant material before placing it into the jars largely reduced, though did not exclude totally, the possibility that adults using the plants only as food or refuge remained in the sample. Furthermore, this rearing method did not prevent us obtaining adults that developed as larvae in the short shoots of the samples. The larvae of most species pupated and developed to adults in the collected plant material. Those that emerged as fully grown larvae were put into separate glass jars with steamed soil for pupation. Unfortunately, the mortality of these larvae was high. All emerging adults were collected and preserved for identification. The jars were kept at room temperature until autumn, afterwards they were transferred to an open air insectary for overwintering. The jars were repeatedly checked for emerging insects for at least one year.

The taxonomy of the weevil species dealt with below is based primarily on the works of CALDARA (1990), DIECKMANN (1977, 1988), EHRET (1990), ENDRŐDI (1971), and GYŐRFFY (1956). We use the names of the plant tribes according to the publications of the Royal Botanical Gardens, Kew (POLHILL & RAVEN 1981), while the plant species names correspond to those in the work by TUTIN *et al.* (1978) with the exception of *Vicia angustifolia* that is regarded below as a separate species while according to TUTIN *et al.* it is only a subspecies of *Vicia sativa.*

RESULTS AND DISCUSSION

The biology of several weevil species, especially those developing in wild plants, is still very poorly known. Most literature sources are restricted to data on the collection of adults on certain plant species without rearing them from the plants, so the biology of the larvae remained unknown. As our rearing method did not exclude totally to get also adults that may have developed as larvae in the shoots or buds, in Table 1 we have marked with * those species for which seed predation can only be supposed by analogy of closely related species, though has not been proved yet.

The biology of the larvae of *Exapion corniculatum* was unknown earlier (DIECKMANN 1977). PODLUSSÁNY (1981) found, however, that the larva developed to adult within a single seed of *Lembotropis nigricans*. All *Tychius* spp. are most likely seed predators as, according to CALDARA (1990), no other types of larval feeding has been observed in this genus so far.

We collected samples at 148 sites (Table 2) from 139 species and subspecies of Leguminosae equalling roughly 86% of all known legume taxa of the Hungarian flora. Interestingly, only 54 species (38.8% of all sampled species) (Table 3) turned out to harbour weevils representing 43 species (Table 1). The host plant affiliation of weevil species found can be characterised as follows.

Table 1. Leguminous host plants of seed predator weevil species in Hungary

Weevil species[1]	Host plant species	Location codes[2] (No of samples)[3] References[4]
Cyanapion (Bothryorrhynchapion) platalea (GERMAR)	*Lathyrus tuberosus*	51, D, E
**Eutrichapion (Cnemapion) gribodoi* DESBROCHERS	*Galega officinalis*	92(2), D, E
Eutrichapion (Psilocalymma) punctigerum PAYKULL	*Vicia angustifolia*	19(3), 82, D, E
Exapion compactum (DESBROCHERS)	*Genista pilosa*	65, 142, D, E
Exapion corniculatum (GERMAR)	*Chamaecytisus austriacus*	102, 132
	Chamaecytisus supinus	46, 115, 138, D, E
	Genista tinctoria	42, 77(2), 81(2), 83, 105
	Lembotropis nigricans	82, 90(2), 139, D, E
Exapion difficile (HERBST)	*Genista tinctoria*	41, 42, 48, 51, 72, 77, 81(2), 115, D
Exapion elongatulum (DESBROCHERS)	*Chamaecytisus austriacus*	81(6)
	Chamaecytisus supinus	38, 46, 48, 64. 81(3), 115, 140, 141, D, E
	Genista tinctoria	106, D, E, G
Exapion formaneki (WAGNER)	*Chamaecytisus supinus*	47, D, E
	Genista tinctoria	47, 81, 115, D, E, G
Exapion fuscirostre (FABRICIUS)	*Cytisus scoparius*	33, 112(2), 114, 121, 138, 142, 147, D, E, G
Holotrichapion ononis (KIRBY)	*Ononis hircina*	1, E, G
	Ononis spinosa	9, 78, 96, 111, 112, 138, D, E, G
Ischnopterapion aeneomicans (WENCKER)	*Dorycnium pentaphyllum*	94, 90, D
Ischnopterapion loti (KIRBY)	*Dorycnium pentaphyllum*	54, D
	Lathyrus pratensis	72
	Lotus corniculatus	1, 10, 13, 16, 19(2), 20, 22, 23, 31, 36, 38, 40, 42, 49, 54, 64, 72(5), 74(2), 76(4), 77(2), 81, 82(10), 94(3), 97, 103, 110, 113(2), 118, 120, 124, 131, 136, 139, 141, 143, 145, D, E, J-B
	Lotus tenuis	119, D, E
	Medicago falcata	95
	Vicia tetrasperma	77, 83
Mesotrichapion punctirostre (GYLLENHAL)	*Astragalus asper*	67, D, E
	Astragalus onobrychis	16, D, E, G
Oxystoma cerdo (GERSTAECKER)	*Vicia angustifolia*	82
	Vicia cracca	22, 42, 76(2), 77, 110, D, E, G

Table 1 (continued)

Weevil species[1]	Host plant species	Location codes[2] (No of samples)[3] References[4]
Oxystoma cerdo (GERSTAECKER)	*Vicia tenuifolia*	19, 22, 26, 36, 41, 42, 44, 81(8), 90(2), 128, D, E
	Vicia villosa	35, D, E
Oxystoma craccae (LINNAEUS)	*Vicia hirsuta*	12(2), 13, 28, 83, 94, 116, D, E
**Oxystoma dimidiatum* (DESBROCHERS)	*Vicia villosa*	134
Oxystoma ochropus (GERMAR)	*Vicia grandiflora*	11, 13, 63, 117
	Vicia sepium	18, 83(2), 123, 148, D, E, G
	Vicia sparsiflora	87(2), 105, 106(2)
	Vicia tenuifolia	81(2)
Oxystoma pomonae (FABRICIUS)	*Vicia angustifolia*	12, 19(7), 24, 68(2), 82(8), 95 D, E
	Vicia sativa	19, D, E
Oxystoma subulatum (KIRBY)	*Astragalus glycyphyllos*	72
	Lathyrus pratensis	22, 30, 34, 42, 50, 64, 69, 70, 71, 72, 73(2), 74, 75, 76(3), 88, 93, 101, 104, 120, 123(2),136, D, E, G
	Lotus corniculatus	72, J-B, G
Protapion apricans (HERBST)	*Ononis spinosa*	66
	Trifolium pallidum	37
	Trifolium pratense	11, 19(3), 26, 53, 64, 82, 85, 86, 94, 107, D, E, J-B
	Trifolium rubens	11
	Vicia tetrasperma	107
Protapion assimile (KIRBY)	*Trifolium medium*	26, 31, D, E, J-B
	Trifolium pratense	80, 82, 86, D, E, J-B
Protapion fulvipes (FOURCROY)	*Trifolium angulatum*	24
	Trifolium aureum	64, 72, 76, E
	Trifolium hybridum	15, 53, 63
	Trifolium repens	19(2), 76, 82(2), 86, W
Protapion gracilipes (DIETRICH)	*Trifolium medium*	6, 27a, 37, 42, 52, 61, 72, 76, 107, 118, 146, D, E, G
Protapion nigritarse (KIRBY)	*Trifolium aureum*	67, 82, D, E
	Trifolium campestre	45, 94, 97, D, E
Protapion ononidis (GYLLENHAL)	*Ononis hircina*	1, 13, G
	Ononis spinosa	3, 5, 7, 25, 38, 59, 66, 96, 99, 108 118, 129, 138, D, E, G
Protapion ruficrus (GERMAR)	*Trifolium alpestre*	81, 84, D, E
**Protapion schoenherri* (BOHEMAN)	*Trifolium striatum*	89
Protapion trifolii (LINNAEUS)	*Trifolium alpestre*	84
	Trifolium fragiferum	13

Table 1 (continued)

Weevil species[1]	Host plant species	Location codes[2] (No of samples)[3] References[4]
Protapion trifolii (LINNAEUS)	*Trifolium medium*	13, 26, 42, 107, 134, D
	Trifolium ochroleucon	43, D
	Trifolium pannonicum	123
	Trifolium pratense	11, 19, 34, 53, 64, 107, 125(2), D, J-B
Protapion varipes (GERMAR)	*Trifolium pratense*	32, D, E, J-B
Pseudoprotapion astragali (PAYKULL)	*Astragalus glycyphyllos*	27a, 51, 135, D, E, G
Tychius breviusculus DESBROCHERS	*Melilotus officinalis*	98, C, D
**Tychius caldarai* DIECKMANN	*Lotus corniculatus*	113, D
**Tychius cuprifer* (PANZER)	*Trifolium repens*	82, D
Tychius flavus BECKER	*Dorycnium pentaphyllum*	132
	Lotus corniculatus	40, 94, 113
	Medicago falcata	128, C, D
Tychius junceus (REICH)	*Dorycnium pentaphyllum*	79, 132
	Medicago falcata	128
	Medicago prostrata	55
Tychius kulzeri PENECKE	*Dorycnium pentaphyllum*	25, 54, 132, C, D
	Lotus corniculatus	94
Tychius picirostris (FABRICIUS)	*Medicago falcata*	95
	Trifolium hybridum	63, 127, C, D
	Trifolium pratense	34, ES
	Trifolium repens	19, 82(2), C, D, W
Tychius quinquepunctatus (LINNAEUS)	*Genista tinctoria*	103
	Lathyrus latifolius	81(4), 128, C
	Lathyrus niger	43
	Lathyrus nissolia	61, 84
	Lathyrus pannonicus	81(2)
	Lathyrus pratensis	12, C, D
	Lathyrus sylvestris	74, C, D
	Lathyrus tuberosus	86, 90, J-B
	Pisum sativum	86, C, D, J-B
	Vicia angustifolia	12, 19(8), 24, 58, 60, 68(2), 82(11), 83, 86, 110, C, J-B
	Vicia cassubica	62
	Vicia cracca	14, 19(2), 27, 36, 136, 144, C, D
	Vicia grandiflora	11, 83(2), 107
	Vicia pannonica	94, 107, 113, 133
	Vicia sepium	83, C, D, J-B
	Vicia tenuifolia	90(2), 128, C, D
	Vicia tetrasperma	29

Table 1 (continued)

Weevil species[1]	Host plant species	Location codes[2] (No of samples)[3] References[4]
Tychius schneideri (HERBST)	*Anthyllis vulneraria* ssp. *polyphylla*	17, 21, 54, 56, 80, 132(3), 137, C, D, ES
Tychius squamulatus GYLLENHAL	*Lotus corniculatus*	1, 16, 19, 23, 40, 49, 54, 77, 83, 94(2), 113, C, D
**Tychius subsulcatus* TOURNIER	*Astragalus onobrychis*	16, C
**Tychius tibialis* BOHEMAN	*Trifolium striatum*	89, D
Tychius trivialis BOHEMAN	*Astragalus cicer*	98, C, D
	Astragalus exscapus	122
	Astragalus glycyphyllos	2, C, D

[1]Species marked with * are also most likely seed predators, although their biology is not exactly known [According to CALDARA (1990) all *Tychius* species are seed predators]

[2]See Table 2

[3]If more than one sample was taken at the given site from several plant stands or in different years

[4]Only publications containing data on host plant species are referred to. Publications mentioning plant genera only (e.g. "*Trifolium* spp.") have not been considered. C = CALDARA 1990; D = DIECKMANN 1977, 1988; E = EHRET 1990; ES = ENDRŐDI 1971; G = GYŐRFFY 1956; J-B = JERMY & BALÁZS 1990; W = WIECH & WUNK 1985

Table 2. Sites of collection of Leguminosae samples

Locality	Habitat[1]	Code
Acsalag (Földsziget)	hydric grassland	1
Aszód	roadside	2
Baja		3
Bakonybél	forest edge	4
Bakonybél	pasture	5
Bakonycsernye	oak-forest edge	6
Bakonyszűcs	pasture	7
Balatongyörök		9
Balatonszéplak	sandy edge of ditch	10
Barabás, Kaszonyi-hegy		11
Battonya, Tompapuszta	loess grassland	12
Bátorliget	hydric pasture	13
Bikács, Ökör-hegy	forest edge	14
Bogdása	forest understory	15
Budakeszi reptér	pasture and waste ground	16
Budaőrs, Út-hegy		17
Budapest, Feketefej	hornbeam-oak-forest understory	18
Budapest, Óbuda	abandoned orchard	19
Budapest, Pesthidegkút	grassland	20
Budapest, Sas-hegy	xeric grassland	21
Budapest, Sváb-hegy		22

Table 2 (continued)

Locality	Habitat[1]	Code
Bugac		23
Csanádpalota, Blaskovicspuszta	sodic grassland	24
Csákvár, Haraszt-hegy	xeric pasture	25
Csákvár, Vásár-hegy	forest edge	26
Csévharaszt	grassland	27
Csopak, Nosztori-völgy		27a
Csörötnek	brook bank	28
Csörötnek	grassy forest edge	29
Devecser	hydric grassland	30
Dömös, Vadálló-kövek		31
Drávaiványi	forest understory	32
Drávatamási	pine-forest edge	33
Egerbakta-Sirok	edge of xeric oak-forest	34
Farkasfa	pine-forest clearing	35
Felnémet	loess grassland	36
Felsőszölnök	grassland	37
Fenyőfő	pine-forest edge	38
Fót, Somlyó	xeric grassland	39
Füzérradvány	country house park	40
Galyatető	shrubby grassland	41
Galyatető	roadside	42
Gyöngyössolymos	shrubby clear-cut forest	43
Győrszentiván	grassland	44
Gyulafirátót	pasture road	45
Gyulafirátót	pasture	46
Hárskút	forest edge	47
Hárskút	pasture	48
Hortobágy	sodic grassland	49
Hortobágy, Nyírőlapos		50
Isztimér	oak-forest understory	51
Isztimér	roadside in a beech-forest	52
Jánd	mesic grassland	53
Kádárta	xeric grassland	54
Kádárta	black pine-forest edge	55
Kádárta		56
Kákics	grassland	57
Kápolna	old-field	58
Keszthely, Apró-hegyek		59
Kisgyőr		60
Komló, Zobák-bánya	pine-forest edge	61
Komló, Zobák-bánya	forest edge	62
Kömörő	forest understory	63

Table 2 (continued)

Locality	Habitat[1]	Code
Kőszegi-hegység	forest roadside	64
Kőszegi-hegység	chestnut-oak forest edge	65
Kunpeszér	hydric grassland	66
Kunszentmiklós, Apajpuszta	sodic grassland	67
Litér	pasture	68
Mátraháza, Tetves-rét	oak-forest clearing	69
Mátraszentimre	roadside	70
Mátraszentimre, Kút-hegy.	shrubby mesic grassland	71
Mátraszentimre, Bagolyirtás	shrubby mesic grassland	72
Mátraszentimre, Bőgős-rét	hydric forest clearing	73
Mátraszentimre, Darázs-hegy	beech-forest clearing	74
Mátraszentimre, Nárád-patak	beech-forest edge	75
Mátraszentistván	shrubby mesic grassland	76
Mátraszentlászló, Piszkés	mesic grassland	77
Meggyeskovácsi	pasture	78
Nagyharsány		79
Nagyharsány	mesic grassland	80
Nagykovácsi	xeric Turkey-oak-forest edge	81
Nagykovácsi	old-field	82
Nagykovácsi	shrubby mesic grassland	83
Nagykovácsi	Turkey-oak-forest edge	84
Nagykovácsi	Turkey-oak-forest understory	85
Nagykovácsi	cultivated field	86
Nagykovácsi, Remete-hegy	oak-forest understory	87
Nagytárkánypuszta, Csabrendek	hydric grassland	88
Nagyvázsony	xeric grassland	89
Noszvaj, Síkfőkút	oak-forest edge	90
Nyírád	brook bank	91
Nyírád	oak-forest edge	92
Nyírád	hydric grassland	93
Óbánya	old-field	94
Óbudavár	mesic grassland	95
Óbudavár	forest clearing	96
Ohati-erdő, Egyek	oak-forest clearing	97
Örkény	roadside	98
Öskü	pasture	99
Padragkút	oak-forest understory	100
Padragkút	hydric grassland	101
Pilisszántó	loess grassland	102
Pilisszenlélek		103
Pilisszentlászló	grassland	104
Pomáz, Csikóváralja		105
Pomáz, Csikóvár		106

Table 2 (continued)

Locality	Habitat[1]	Code
Pula	forest edge	107
Pula	grassland	108
Pusztaszer	pasture	109
Recsk	xeric pasture	110
Révfülöp	abandoned orchard, roadside	111
Rezi	pasture	112
Romhány	xeric shrubby grassland	113
Sümeg	pasture	114
Súr	pasture	115
Szalafő, Pityerszer	grassland adjacent cultivated fields	116
Szalafő, Pityerszer	grassland	117
Szalafő	grassland	118
Szentendrei sziget, Kisoroszi	hydric grassland	119
Szentpéterfölde		120
Szőce	pine-forest edge	121
Sződliget	railway bed	122
Tahi, Kalicsa-völgy	forest edge	123
Tápiószele	cultivated	124
Terecsenypuszta, Sas-rét	forest meadow	125
Tiszapüspöki	xeric grassland	126
Tokaj, Tisza-part	river bank	127
Tokaji-hegy	pine- and oak-forest understory	128
Ugod	pasture	129
Úrkút	oak-forest edge	130
Üllés	mesic grassland	131
Üröm	xeric limestone grassland	132
Üröm	edge of cultivated fields	133
Üröm, Nagykevély	xeric grassland	134
Vállus	xeric grassland	135
Várad, Sikota-puszta	forest edge	136
Várpalota	xeric dolomitic grassland	137
Várvölgy	pasture	138
Vászoly	xeric scrub vegetation	139
Vászoly	abandoned orchard	140
Velem	vineyard	141
Velem	roadside, oak and chestnut trees	142
Verpelét	mesic grassland	143
Vörs, Kis-Balaton	lake shore	144
Zalaszántó, Tátika		145
Zirc	pasture	146
Zirc		147
Zsófiapuszta, Úrkút	oak-forest edge	148

[1]At some localities the character of the habitat is lacking mostly because the samples were taken by other persons and the habitat could not been recalled exactly later

Table 3. Number of weevil species per plant species

Plant tribes and species	Weevil species	No. of infested samples	No. of samples collected
Tribe Galegeae			
Astragalus asper	*M. punctirostre*	1	3
A. cicer	*T. trivialis*	1	28
A. exscapus	*T. trivialis*	1	4
A. glycyphyllos	*O. subulatum*	1	66
	P. astragali	3	
	T. trivialis	1	
A. onobrychis	*M. punctirostre*	1	19
	T. subsulcatus	1	
Galega officinalis	*E. gribodoi*	2	7
Tribe Loteae			
Anthyllis vulneraria ssp. *polyphylla*	*T. schneideri*	9	26
Dorycnium pentaphyllum	*I. aeneomicans*	2	16
	I. loti	1	
	T. flavus	1	
	T. junceus	2	
	T. kulzeri	3	
Lotus corniculatus	*I. loti*	58	80
	O. subulatum	1	
	T. caldarai	1	
	T. flavus	3	
	T. kulzeri	1	
	T. squamulatus	12	
L. tenuis	*I. loti*	1	3
Tribe Vicieae			
Lathyrus latifolius	*T. 5-punctatus*	5	27
L. niger	*T. 5-punctatus*	1	26
L. nissolia	*T. 5-punctatus*	2	9
L. pannonicus	*T. 5-punctatus*	2	8
L. pratensis	*I. loti*	1	65
	O. subulatum	25	
	T. 5-punctatus	1	
L. sylvestris	*T. 5-punctatus*	1	33
L. tuberosus	*C. platalea*	1	55
	T. 5-punctatus	2	
Pisum sativum	*T. 5-punctatus*	1	12
Vicia angustifolia	*E. punctigerum*	4	116
	O. cerdo	1	
	O. pomonae	1	
	T. 5-punctatus	28	
V. cassubica	*T. 5-punctatus*	1	28

Table 3 (continued)

Plant tribes and species	Weevil species	No. of infested samples	No. of samples collected
Vicia cracca	*O. cerdo*	6	44
	T. 5-punctatus	7	
V. grandiflora	*O. ochropus*	4	25
	T. 5-punctatus	4	
V. hirsuta	*O. craccae*	7	22
V. pannonica ssp. *pannonica*	*T. 5-punctatus*	4	12
V. sativa ssp. *sativa*	*O. pomonae*	1	3
V. sepium	*O. ochropus*	5	35
	T. 5-punctatus	1	
V. sparsiflora	*O. ochropus*	5	8
V. tenuifolia	*O. cerdo*	18	78
	O. ochropus	2	
	T. 5-punctatus	3	
V. tetrasperma	*I. loti*	2	10
	P. apricans	1	
	T. 5-punctatus	1	
V. villosa	*O. cerdo*	1	24
	O. dimidiatum	1	
Tribe Trifolieae			
Medicago falcata	*I. loti*	1	14
	T. flavus	2	
	T. junceus	1	
	T. picirostris	1	
M. prostrata	*T. junceus*	1	2
Melilotus officinalis	*T. breviusculus*	1	6
Ononis hircina	*H. ononis*	1	3
	P. ononidis	1	
O. spinosa	*H. ononis*	6	26
	P. apricans	1	
	P. ononidis	13	
Trifolium alpestre	*P. ruficrus*	2	12
	P. trifolii	1	
T. angulatum	*P. fulvipes*	1	1
T. aureum	*P. fulvipes*	3	20
	P. nigritarse	2	
T. campestre	*P. nigritarse*	3	4
T. fragiferum	*P. trifolii*	1	3
T. hybridum	*P. fulvipes*	3	6
	T. picirostris	2	
T. medium	*P. assimile*	2	22
	P. gracilipes	11	
	P. trifolii	5	

Table 3 (continued)

Plant tribes and species	Weevil species	No. of infested samples	No. of samples collected
Trifolium ochroleucum	*P. trifolii*	1	4
T. pallidum	*P. apricans*	1	1
T. pannonicum	*P. trifolii*	1	1
T. pratense	*P. apricans*	12	13
	P. assimile	3	
	P. trifolii	8	
	P. varipes	1	
	T. picirostris	1	
T. repens	*P. fulvipes*	6	7
	T. cuprifer	1	
	T. picirostris	3	
T. rubens	*P. apricans*	1	18
T. striatum	*P. schoenherri*	1	5
	T. tibialis	1	
Tribe Genisteae			
Chamaecytisus austriacus	*E. corniculatum*	2	17
	E. elongatulum	6	
C. supinus	*E. corniculatum*	3	21
	E. elongatulum	10	
	E. formaneki	1	
Cytisus scoparius	*E. fuscirostre*	8	15
Genista pilosa	*E. compactum*	2	2
G. tinctoria	*E. corniculatum*	7	42
	E. difficile	9	
	E. elongatulum	1	
	E. formaneki	3	
	T. 5-punctatus	1	
Lembotropis nigricans	*E. corniculatum*	4	31

Monophagy or at least a very narrow specialisation has been found with the following species (considering only cases when at least 4 plant samples from at least 3 locations were collected): *Exapion difficile* on *Genista tinctoria* (9 samples from 8 locations), *E. fuscirostre* on *Cytisus scoparius* (8 samples from 7 locations), *Oxystoma craccae* on *Vicia hirsuta* (7 samples from 6 locations), *Tychius schneideri* on *Anthyllis vulneraria* ssp. *polyphylla* (9 samples from 7 locations), *T. squamulatus* on *Lotus corniculatus* (12 samples from 11 locations). According to DIECKMANN (1977) *Protapion gracilipes* is monophagous on *Trifolium medium*. This has been supported strongly by our data (11 samples from 11 locations).

It is important to note that all *Exapion* spp. were reared exclusively from genera belonging to one plant tribe: Genisteae (altogether 56 samples from 28 locations).

The species of *Protapion* are strongly specialised to *Trifolium* spp. Namely, 8 from the 10 species emerged exclusively from *Trifolium* spp. (56 samples from 34 locations). The exceptions are as follows: *P. ononidis* occurred on *Ononis* spp. (15 samples from 15 locations); *P. apricans* occurred, as well as on *Trifolium* spp. (14 samples from 12 locations), also on *Ononis spinosa* and *Vicia tetrasperma* (1 sample each). That means that *Protapion* spp. use mostly plant species of the tribe Trifolieae.

A less narrow specialisation prevails in the genus *Oxystoma,* though *Vicia* spp. occur most often among the host plants followed by *Lathyrus* spp. In detail, *O. cerdo, O. craccae* (not found in *Vicia cracca*!), *O. dimidiatum, O. ochropus,* and *O. pomonae* occurred only in *Vicia* spp. (71 samples from 23 locations). *O. subulatum* occurred, as well as on *Lathyrus pratensis* (25 samples from 21 locations), also on *Lotus corniculatus* and on *Astragalus glycyphyllos* (1 sample each). Thus, *Oxystoma* species were associated mostly with species of Vicieae, but sporadically also with species of Galegeae and Loteae.

A relatively broad host plant range (5 genera of 3 tribes) characterised *Ischnopterapion loti*, although it was mostly found in *Lotus* spp. (59 samples from 37 locations) while it was present in only one sample each of *Dorycnium pentaphyllum, Lathyrus pratensis, Medicago falcata* and in two samples of *V. tetrasperma.*

The species of *Tychius* showed a most variable host affiliation. Unfortunately, most species were found only in a few samples, therefore in most cases further investigation is necessary to get a better picture of host affiliation in this genus. Taking into consideration only species that were reared from at least 4 samples from at least 3 locations, there seems a decisive specialisation in *T. picirostris* to *Trifolium* spp. (6 samples from 5 locations) while *Medicago falcata* is represented only by one sample and, as mentioned before, in *T. schneideri* to *Anthyllis vulneraria* ssp. *polyphylla* (9 samples from 7 locations). On the other hand, several species use plant species of quite far related plant genera such as *T. flavus* (3 genera of 2 tribes) and *T. quinquepunctatus* (4 genera of 2 tribes).

In conclusion, the host plant specialisation of the seed predator weevil species shows a very variable picture from possible monophagy or at least ecological monophagy (FOX & MORROW 1981) to narrow oligophagy and to a broader host range such as in *Ischnopterapion loti*: species of 5 plant genera belonging to 3 tribes.

Besides the host plant species listed in Table 1 we have reared the following weevil species from plant species that seem "unusual" as they contradict both the

majority of our rearing data and the available literature data. They need further investigation the more so as we have reared only *one* adult of each species from these plants: *Oxystoma cerdo* from *Chamaecytisus supinus, Protapion ruficrus* from *Trifolium ochroleucon* and *Tychius quinquepunctatus* from *Astragalus glycyphyllos*.

As for the number of curculionid species per plant species (Table 3), it is remarkable that among the 54 plant species found as hosts, 29 and 11 species (i.e., 53.7 + 20.4 = 74.1%) were infested only by one and two weevil species, respectively, while the maximum of 6 species occurred only in *Lotus corniculatus*. Furthermore, in about two-third of the host plant species, weevils emerged from less than half of all samples collected. Considering also the fact that seed predator weevils occurred only in 38.8% of the sampled leguminous species, it can be concluded that the rate of resource exploitation by these insects is quite low at the plant species level.

*

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REFERENCES

CALDARA, R. (1990) Revisione tassonomica delle specie paleartiche del genere Tychius Germar (Coleoptera Curculionidae). *Mem. Soc. Ital. Sci. Nat. Museo Civ. Storia Nat. Milano* **25**(3): 51–218.

COLONNELLI, E. & OSELLA, G. (1998) Host and refuge plants of weevils (Coleoptera: Curculionidea). Taxonomy, ecology and distribution of Curculionoidea. XX. C. I. E. (1996, Firenze, Italy). *Mus. reg. Sci. nat. Torino* **1998**: 191–216.

DIECKMANN, L. (1977) Beiträge zur Insektenfauna der DDR: Coleoptera Curculionidae (Apioninae). *Beitr. Entomol.* **27**: 7–143.

DIECKMANN, L. (1988) Beiträge zur Insektenfauna der DDR: Curculionidae, (Curculioninae: Ellescini, Acalyptrini, Tychiini, Anthonomiini, Curculionini). *Beitr. Entomol.* **35**: 356–468.

EHRET, J.-M. (1990) Les Apions de France: clés d'identification commentées (Coleoptera Curculionidae Apioninae). *Bull. mens. Soc. linn. Lyon* **59**: 209–292.

ENDRŐDI, S. (1971) *Curculionidae – Ormányosbogarak V. Fauna Hung.* Akadémiai Kiadó, Budapest, 10(8): 1–167.

FOX, L. R. & MORROW, P. A. (1981) Specialization: species property or local phenomenon? *Science* **211**: 887–893.

GYŐRFFY, J. (1956) *Apionidae – Cickányormányosok. Fauna Hung.* Akadémiai Kiadó, Budapest, 10(3): 1–56.

JERMY, T. & BALÁZS, K. (eds) (1990) *A növényvédelmi állattan kézikönyve. 3.* [Handbook of Agricultural Entomology, Vol. 3.] Akadémiai Kiadó, Budapest, 473 pp.

PODLUSSÁNY, A. (1981) Exapion fajok előfordulása a Bakony hegységben (Col., Apionidae III.) (Vorkommen von Exapion Arten im Bakony Gebirge). *Veszprém Megyei Múzeumok Közleményei* **16**: 129–136.

POLHILL, R. M. & RAVEN, P. H. (eds) (1981): *Advances in legume systematics.* Royal Botanic Gardens, Kew, England, XVI + 1049 pp.

TUTIN, T. G., HEYWOOD, V. H., BURGES, N. A., MOORE, D. M., VALENTINE, D. H., WALTERS, S. M. & WEBB, D. A. (eds) (1978) *Flora Europaea. Vol. 2. Rosaceae to Umbelliferae.* Cambridge Univ. Press, XXVII + 455 pp.

WIECH, K. & WUNK, A. (1985) O szkodliwosci ryjkowców Apion flavipes (Payk.) i Miccotrogus picirostris (F.) na krajowich odmianach koniczyny bialej. *Acta Agraria et Silvestria, Agraria, Kraków* **24**: 219–225.

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A DESCRIPTION OF THE SONG OF PHOLIDOPTERA TRANSSYLVANICA (FISCHER-WALDHEIM, 1853) (ORTHOPTERA: TETTIGONIIDAE)

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The song of *Pholidoptera transsylvanica*, a (sub-)endemic bush-cricket of the Carpathian Basin, is described for the first time. The songs of 9 specimens from Hungary and Transylvania (Romania) have been analysed. The stridulatory file was 3.9–4.3 mm long and contained 106–121 stridulatory pegs (a scanning electron microscopic photo of the stridulatory file is presented). Oscillographic analysis showed that the song is composed of regularly or sporadically repeated trisyllabic echemes. The duration of echemes was temperature dependent ($r = -0.9881$, $p<0.001$) $D = -13.39 * T + 456.69$ [where D is the duration of echeme in ms and T is the ambient air temperature in °C between 21 and 28 °C]. Echeme-repetition rate varied widely (23–133 echemes per minute at 26–28 °C). The relationship between the song of *Ph. transsylvanica* and that of the other species of *Pholidoptera* occurring in the Carpathian Basin is discussed.

Key words: Pholidoptera transsylvanica, song, oscillogram, stridulatory file

INTRODUCTION

Sound communication plays an important role in the mate finding behaviour of many orthopteran insects. Males advertise themselves by emitting sound signals which convey information about their species identity (e.g., WALKER 1957, DOBLER *et al.* 1994, TAUBER & PENER 2000) and personal properties such as body size (LATIMER 1981, SIMMONS 1988, BROWN *et al.* 1996), or age (STEIDL *et al.* 1991). Conspecific females use this information to decide which male to approach or attract by responding. Thus sound signals function as important elements of the species recognition system of these insects (PERDECK 1958, BAILEY & ROBINSON 1971, GWYNNE & MORRIS 1986), which makes it relevant and often highly effective to study these signals for solving taxonomic problems in morphologically uniform groups of sibling species (e.g., RAGGE & REYNOLDS 1988). On the other hand these signals have become the preferred objects of behavioural ecological studies on sexual selection (see again e.g., SIMMONS 1988, BROWN *et al.* 1996), host selection of sound oriented parasites (e.g., ALLEN 1995, ZUK *et al.* 1995), predator avoidance (BELWOOD & MORRIS 1987) and prey localisation (WALKER 1964, GUIDO & FOWLER 1988). Furthermore orthopteran songs can be used to de-

tect specimens by researchers, using their unaided ear (FISCHER *et al.* 1997) or high-frequency sound detectors (BOONMAN 1995), for estimating the population size of threatened species. From the above mentioned examples it is obvious that the knowledge of the acoustic signals of orthopteran insects constitutes a fundamental part of their natural history.

Pholidoptera is one of the most familiar genera of the Decticinae bush-crickets including 15–20 species in Europe [at present the status and validity of some species from the Balkan Peninsula is doubtful (HARZ 1969, HELLER 1988, NASKRECKI & OTTE 1999)]. They live on or near the ground level of grasslands or in shrubs. Wings are reduced in both sexes. Their cautious behaviour and cryptic coloration often make their visual detection difficult, while their songs are often conspicuous, especially during the rivalry singing of neighbouring males (JONES 1966). The songs of most European species have been studied and subjected to oscillographic analysis. The most comprehensive summary of our knowledge on the songs of this genus can be found in the excellent works of HELLER (1988) and RAGGE & REYNOLDS (1998). *Pholidoptera transsylvanica* is known as a (sub-)endemic species of the Carpathian Basin [see RÁCZ (1998) for a distribution map] somewhat expanding its area to the northern part of the Balkan Peninsula (US & MATVEJEV 1967). It is one of the few European species in which we do not know of any published information on the song. The aim of this study is to fill this gap in our knowledge of the bioacoustics of the European species of *Pholidoptera*.

MATERIAL AND METHODS

Songs of the following males were recorded and analysed: 2 males (near Rimetea , Torockói Mountains, Transylvania, Romania), 1 male (near the village Barabás, Kaszonyi-hegy [hill], NE Hungary), 3 males (near the village Telkibánya, Zemplén Mountains, NE Hungary), 3 males (near the village Jósvafő, Aggtelek Karst, NE Hungary). The stridulatory file was examined in the six males from the Zemplén Mountains and Aggtelek Karst. Data on the specimens of the other *Pholidoptera* species of which the song is illustrated by oscillograms in Figure 3 can be found in Table 1.

Recordings were made using a Sony TCD-D7 DAT-recorder (working at 48 kHz sampling frequency) with a Monacor ECM 920 electret condenser microphone. Recordings were transferred to a PC equipped with a Sound Blaster 16 sound card. Oscillographic analysis and high pass filtering (Bessel, cut off frequency was set to 50 Hz) were carried out using the software Cool Edit Pro. All recordings were made indoors between 21.7–25.8 °C except for the song of the specimen near Barabás which was recorded in the field at an air temperature of 28 °C. See Table 1 for more detailed data on the recordings which are illustrated by oscillograms in Figures 2 and 3.

I used a Studar M stereo microscope that has a movable stage and was equipped with a graduated eyepiece to examine the morphology of the stridulatory file. Wart-like protuberances and irregularly shaped, alinearly arranged pegs were excluded when counting the number of stridulatory pegs and measuring the length of the stridulatory file. The photo in Figure 1 was taken of a dried, gold-coated stridulatory file by a Hitachi S–2360N scanning electron microscope.

Table 1. Data for the circumstances of the sound-recordings that are illustrated by oscillograms in this study

Species	Date recorded	Locality	Collected by	Temperature	Oscillogram
Ph. transsylvanica	15.viii.1999	Aggtelek Karst (Hu)	KMO	21.7 °C	Fig. 2/A,B
	12.viii.1999	Zemplén Mts (Hu)	IAR&ZV	25.1 °C	Fig. 2/C
	28.vii.1999	Torockói Mts (Ro)	NB	25.8 °C	Fig. 2/D
Ph. fallax	16.x.1999	Budai Mts (Hu)	KMO	21.8 °C	Fig. 3/A
Ph. griseoaptera	16.x.1999	Budai Mts (Hu)	KMO	21.8 °C	Fig. 3/B
Ph. aptera	12.viii.1999	Aggtelek Karst (Hu)	KMO	25.1 °C	Fig. 3/C
Ph. littoralis	28.vii.1998	Gyula (Hu)	NB	25.5 °C	Fig. 3/D
Ph. frivaldskyi	23.viii.1999	Lőcsei Mts (Slo)	GSZ	21.4 °C	Fig. 3/E

Abbreviations: NB – B. NAGY, IAR – I. A. RÁCZ, ZV – Z. VARGA, GSZ – G. SZÖVÉNYI, KMO – K. M. ORCI

Hu – Hungary, Ro – Romania, Slo – Slovakia

The following set of terms was used, accordingly to RAGGE and REYNOLDS (1998), for the description of the song:

Calling song: spontaneous song produced by an isolated male.

Rivalry song: a special song produced by two or more males reacting to one another.

Echeme: a first-order assemblage of syllables.

Syllable: the song produced by one opening-closing movement cycle of the elytra.

Hemisyllable: the song produced during the opening (opening hemisyllable) or during the closing movement (closing hemisyllable) of the elytra. (In *Ph. transsylvanica* I could not make a detailed study on the wing-movement pattern of the stridulating male, so I determined these song-elements by observing the stridulatory movements of some males singing at lower temperatures, and on the basis of the results published on closely related tettigoniid species [see e.g., MORRIS & PIPHER 1972, HELLER 1988]).

Pulse: a simple, undivided, transient train of sound waves (here: the sound impulse arising as the impact of one tooth of the stridulatory file of the male).

RESULTS

Song production was observable only in the males. The song is produced by rubbing the stridulatory file, a series of stridulatory pegs emerging from the underside surface of the vein Cu_2 of the left elytron, against a scraper on the right elytron. In the examined specimens the stridulatory file contained 106–121 pegs (mean = 113.3, n = 6) and a varying number of irregularly arranged wart-like protuberances at both ends. The length of the stridulatory file varied from 3.9 to 4.3 mm (mean 4.08 mm, n = 6). The density of pegs showed little variation throughout the file.

Peg-size increased slightly and gradually from the ends of the file and reached its maximum in the proximal third of the file (Fig. 1).

The basic element of the song is a short, loud, trisyllabic echeme (Fig. 2/B, C, D). Echeme duration showed highly significant correlation with ambient air temperature a ($r = -0.9881$, $p<0.001$, $n = 6$). In the temperature range of 21–28°C the duration of echeme can be described as $D = -13.39 \times T + 456.69$ where D is the duration of echeme in ms, and T is the air temperature in °C. The three syllables of an echeme follow each other in quick succession. Each of them is composed of an opening and a closing hemisyllable. The opening hemisyllable is a continuous noise with relatively low amplitude (see Fig. 2/B: oHS). The closing hemisyllable contains a series of distinct pulses (see Fig. 2/B: cHS). While the amplitude and length of the opening hemisyllables remains nearly constant, the closing hemisyllables become louder and longer, containing progressively more pulses during the succession of the three syllables of an echeme. The number of pulses varied from 4 to 13 in the first closing hemisyllable, from 10 to 24 in the second one, and from 17 to 27 in the third one. Pulse repetition rate tends to decrease towards the end of the second and third closing hemisyllable. Generally echemes are repeated evenly in long sequences at a rate of 23–133

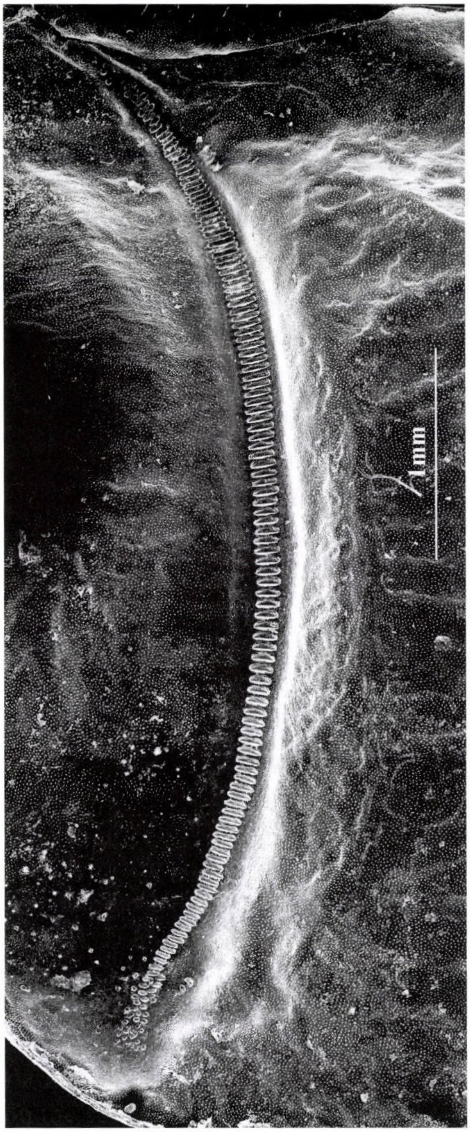


Fig. 1. The stridulatory file of a male of *Pholidoptera transsylvanica* from the Zemplén Mountains (NE Hungary). Distal end of the file is at the bottom of the figure

echemes per minute at 26–28 °C; however single echemes, produced sporadically, can also be observed. Undisturbed males sing conspicuously throughout the day and night and their song can be heard by the unaided human ear from a distance of 30–40 m or at even greater distances, when conditions are favourable. The typical form of sound production in this species is the alternate singing of neighbouring males (Fig. 2/A), which is likely to be a rivalry behaviour. Isolated singing occurs relatively rarely in nature and the "calling song" produced during such situations is principally the same as the rivalry one.

Though the Hungarian populations are completely separated from each other and from the Transylvanian population I did not notice any systematic difference in the oscillographic pattern of their songs (Fig. 2/B, C, D) which could indicate the existence of even a slight, dialect-level song variability between these populations of this species. Note, that the air temperature was lower by 3–4 °C during the recording from which the oscillogram in Fig. 2/B was made than during those from which the oscillograms in Figures 2/C, D, hence the difference in their duration.

DISCUSSION

Oscillographic analysis showed that the song of *Pholidoptera transsylvanica* is composed of regularly or sporadically repeated trisyllabic echemes. Taking into consideration this information, the songs of *Pholidoptera* species occurring in the Carpathian Basin can be classified into three groups. In the first group, which includes the song of *Ph. littoralis* (Fig. 3/D) and *Ph. frivaldskyi* (Fig. 3/E), echemes are composed of more than 10 syllables (up to 50–60 syllables). In the second group, that contains the song of *Ph. transsylvanica* (Fig. 2), *Ph. fallax* (Fig. 3/A) and *Ph. griseoaptera* (Fig. 3/B), echemes consist of 2–5 syllables and are repeated as single echemes. In the third group echemes are repeated quickly, forming echeme-sequences of characteristic duration, the only species in the Carpathian Basin, of which the song belongs to this group is *Pholidoptera aptera* (Fig. 3/C).

Besides the above mentioned basic similarity shown by the songs of *Pholidoptera transsylvanica, Ph. fallax* and *Ph. griseoaptera*, the fine oscillographic structure of their echemes is also rather similar. However, while in *Ph. transsylvanica* echemes are always trisyllabic and the opening hemisyllables of each syllable were always observable, in the other two species some of the opening hemisyllables are often absent, furthermore *Ph. griseoaptera* frequently produces di- or tetrasyllabic echemes (see JONES 1966). These subtle oscillographic differences cannot be detected by the unaided human ear, but with some practice, the song of *Ph. transsylvanica* can be distinguished confidently from that of the other two spe-

cies without any equipment, because it sounds much louder and gives an impression of having a lower pitch.

Contrary to the similarity of their songs, from a morphological point of view *Ph. transsylvanica* differs conspicuously from *Ph. fallax* and *Ph. griseoaptera*, and resembles much more *Ph. aptera* regarding the size of body, the coloration of the lateral lobes of pronotum, the length of elytra (in the males) and the length of ovipositor (HARZ 1969). In orthopteran insects the extent of evolutionary divergence in song and morphology often differs conspicuously: several cases have

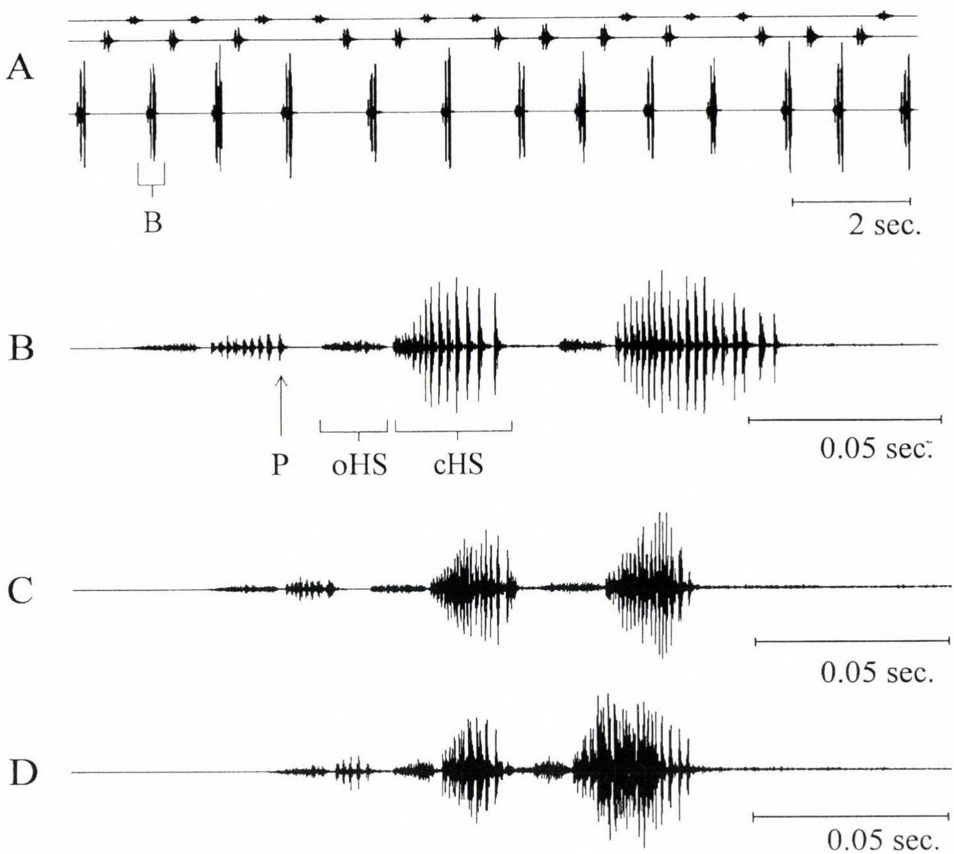


Fig. 2. Oscillograms of the song of *Pholidoptera transsylvanica* – A, a three traced oscillogram showing the timing of alternate singing, the typical form of sound production in this species, of three neighbouring males. B, a faster oscillogram of the echeme indicated in Fig. 2/A, produced by a male from the Aggtelek Karst (NE Hungary) [oHs – opening hemisyllable, cHS – closing hemisyllable, P – the last pulse in the first closing hemisyllable] C, a faster oscillogram of an echeme of a male from the Zemplén Mountains (NE Hungary) D, a faster oscillogram of an echeme of a male from the Torockói Mountains (Transylvania)

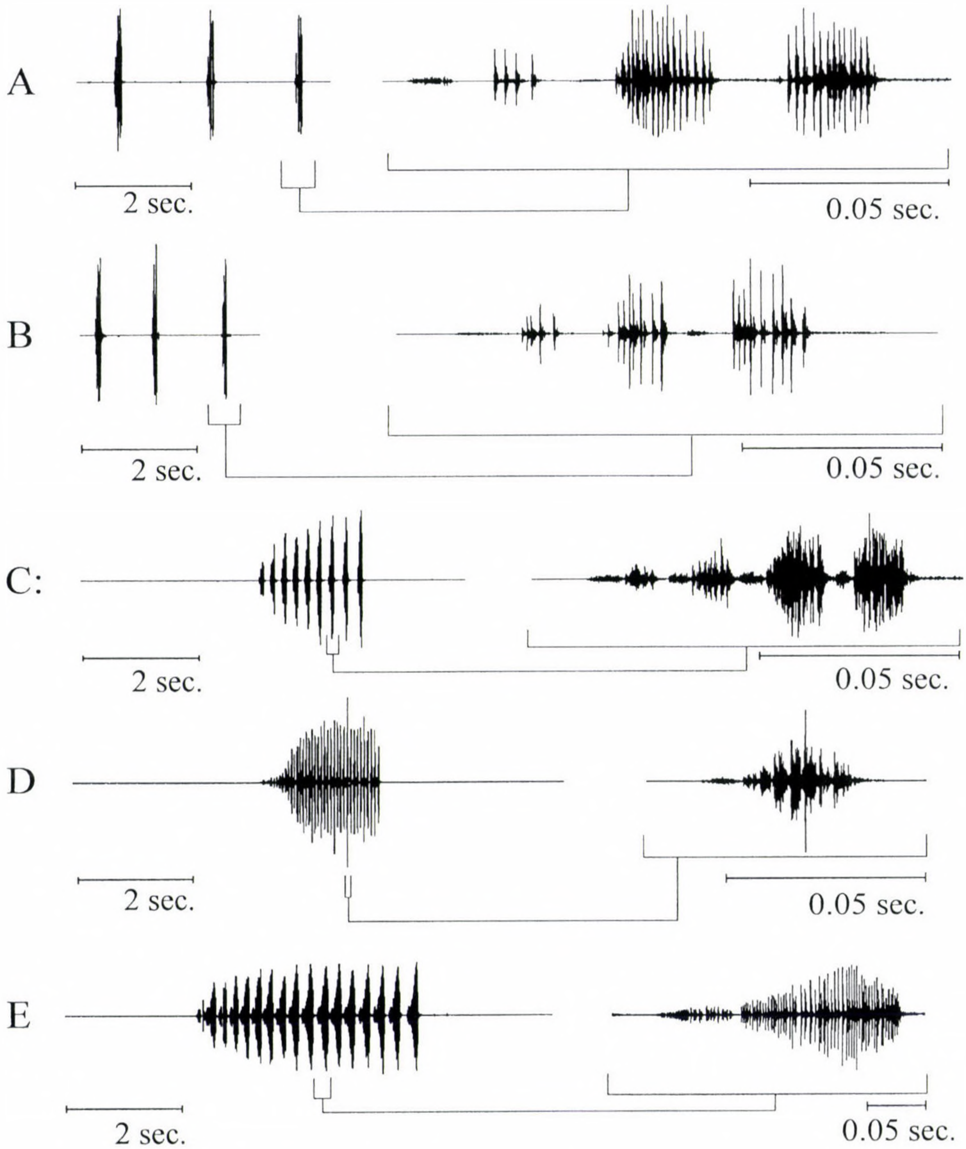


Fig. 3. Oscillograms at two speeds of the songs of the *Pholidoptera* species, which are sympatric with *Ph. transsylvanica* in the Carpathian Basin: A, *Pholidoptera fallax* – three echemes (left) and the faster oscillogram of one of them (right) B, *Ph. griseoaptera* – three echemes (left) and the faster oscillogram of one of them (right) C, *Ph. aptera* – an echeme sequence (left) and the faster oscillogram of one echeme (right) D, *Ph. littoralis* – a single polysyllabic echeme (left) and the faster oscillogram of a syllable (right) E, *Ph. frivaldskyi* – a single polysyllabic echeme (left) and the faster oscillogram of a syllable (right)

been reported when song characters diverged much further than morphological ones (HELVERSEN 1986, RAGGE *et al.* 1990, STUMPNER & HELVERSEN 1994). The similarity of the song of *Ph. transsylvanica*, *Ph. fallax* and *Ph. griseoaptera* provides an example of the opposite situation: in this case song characters are by far less differentiated than morphological ones.

As *Ph. transsylvanica, Ph. fallax* and *Ph. griseoaptera* are not only sympatric but often syntopic in the Carpathian Basin the high degree of similarity shown by their songs raises some questions. How can females distinguish the songs of conspecific and heterospecific males? The spectral properties of the song may be important in these species. How does a male react to the song of a heterospecific male? If heterospecific rivalisation occurs, does it lead to interspecific competition? These questions should be answered by experimental behavioural studies to clarify how the songs of these species function in their mate finding behaviour and whether they play any role during interspecific interactions.

I hope that the information presented in this paper will help entomologists to detect this cautious insect more easily during their field work, and stimulate further behavioural studies on this interesting bush-cricket species.

*

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REFERENCES

ALLEN, G. R. (1995) The calling behaviour and spatial distribution of male bushcrickets (Sciarasaga quadrata) and their relationship to parasitism by acoustically orienting tachinid flies. *Ecol. entomol.* **20**: 303–310.

BAILEY, W. J. & ROBINSON, D. (1971) Song as a possible isolating mechanism in the genus Homorocoryphus (Tettigonioidea, Orthoptera). *Anim. behav.* **19**: 390–397.

BROWN, W. D., WIEDEMAN, J., ANDRADE, M. C. B., MASON, A. C. & GWYNNE, D. T. (1996) Female choice for an indicator of male size in the song of the black-horned tree cricket Oecanthus nigricornis (Orthoptera: Gryllidae: Oecanthinae). *Evolution* **50**(6): 2400–2411.

BELWOOD, J. J. & MORRIS, G. K. (1987) Bat predation and its influence on calling behavior in neotropical katydids. *Science* **238**: 64–65.

BOONMAN, A. M. (1995) A survey method for the speckled bushcricket Lepthophyes punctatissima (Orthoptera: Tettigoniidae) based on its sound emission. *Ent. Ber. Amst.* **55**: 30–35.

DOBLER, S., HELLER, K.-G. & HELVERSEN, O. VON (1994) Song pattern recognition and an auditory time window in the female bushcricket Ancistrura nigrovittata (Orthoptera: Phanetopteridae). *J. Comp. Physiol. A* **175**: 67–74.

FISCHER, F. P., SCHULZ, U., SCHUBERT, H., KNAPP, P. & SCHMÖGER, M. (1997) Quantitative assessment of grassland quality: acoustic determination of population sizes of orthopteran indicator species. *Ecol. appl.* **7**(3): 909–920.

GUIDO, A. S. & FOWLER, H. G. (1988) Megacephala fulgida (Coleoptera: Cicindellidae): a phonotactically orienting predator of Scapteriscus mole crickets (Orthoptera: Gryllotalpidae). *Cicindella* **20**(3/4): 51–52.

GWYNNE, D. T. & MORRIS, G. K. (1986) Heterospecific recognition and behavioral isolation in acoustic Orthoptera (Insecta). *Evol. theory* **8**: 33–38.

HARZ, K. (1969) *Die Orthopteren Europas I.* Series Entomologica Vol. 5, 749 pp.

HELLER, K.-G. (1988) *Bioakustik der europäischen Laubheuschrecken (Ökologie in Forschung und Anwendung 1.).* Margraf, Weikersheim, 358 pp.

HELVERSEN, O VON (1986) Courtship song and taxonomy of grasshoppers in the Chorthippus albomarginatus-group (Orthoptera: Acrididae). *Zool. Jb. Syst.* **113**: 319–342.

JONES, D. R. (1966) The acoustic behaviour of the bush cricket Pholidoptera griseoaptera I. Alternation, synchronism and rivalry between males. *J. Exp. Biol.* **45**: 15–30.

LATIMER, W. (1981) Variation in the song of the bush cricket Platycleis albopunctata (Orthoptera, Tettigoniidae). *J. Nat. Hist.* **15**: 245–263.

MORRIS, G. K. & PIPHER, R. E. (1972) The relation of song structure to tegminal movement in Metrioptera sphagnorum (Orthoptera: Tettigoniidae). *Can. Ent.* **104**: 977–985.

NASKRECKI, P. & OTTE, D. (1999) Orthoptera species file online. http://viceroy.eeb.uconn.edu /Orthoptera

PERDECK, A. C. (1958) The isolating value of specific song patterns in two sibling species of grasshopper (Chorthippus brunneus Thumb. and C. biguttulus L.). *Behaviour* **12**: 1–75.

RAGGE, D. R. & REYNOLDS, W. J. (1988) The songs and taxonomy of the grasshoppers of the Chorthippus biguttulus group in the Iberian Peninsula (Orthoptera: Acrididae). *J. Nat. Hist.* **22**: 897–929.

RAGGE, D. R., REYNOLDS, W. J. & WILLEMSE, F. (1990) The songs of the European grasshoppers of the Chorthippus biguttulus group in relation to their taxonomy, speciation and biogeography. Pp. 239–245. *In* NICKLE, D. A. (ed.) *Proc. 5th Intern. Meeting of the Orthopterists' Society. Bol. San. Veg. Plagas (Fuera de serie) 20.*

RAGGE, D. R. & REYNOLDS, W. J. (1998) *The songs of the grasshoppers and crickets of western Europe.* Harley Books, Colchester, 591 pp.

RÁCZ, I. A. (1998) Biogeographical survey of the Orthoptera fauna in Central Part of the Carpathian Basin (Hungary) – Fauna types and community types. *Articulata* **13**(1): 53–69.

SIMMONS, L. W. (1988) The calling song of the field cricket, Gryllus bimaculatus (De Geer): constraints on transmission and its role in intermale competition and female choice. *Anim. behav.* **36**: 380–394.

STEIDL, O., BICKMEYER, U. & KALMRING, K. (1991) Tooth impact rate alteration in the song of males of Ephippiger ephippiger Fiebig (Orthoptera, Tettigoniidae) and its consequences for phonotactic behaviour of females. *Bioacoustics* **3**: 1–16.

STUMPNER, A. & HELVERSEN, O. VON (1994) Song production and song recognition in a group of sibling grasshopper species (Chorthippus dorsatus, Ch. dichrous and Ch. loratus: Orthoptera, Acrididae). *Bioacoustics* **6**: 1–23.

TAUBER, E. & PENER, M. P. (2000) Song recognition in female bushcrickets Phaneroptera nana. *J. Exp. Biol.* **203**(3): 597–603.

US, P. & MATVEJEV, S. D. (1967) *Catalogus Faunae Jugoslaviae. III/6. Orthopteroidea.* Ljubjana. 48 pp.

WALKER, T. J. (1957) Specificity in the response of female tree crickets (Orthoptera: Gryllidae: Oecanthinae) to calling songs of the males. *Ann. Entomol. Soc. Am.* **50**: 626–636.

WALKER, T. J. (1964) Experimental demonstration of a cat locating orthoptera prey by the prey's calling song. *Florida Entomologist* **47:** 163–165.

ZUK, M., SIMMONS, L. W. & ROTENBERRY, J. T. (1995) Acoustically-orienting parasitoids in calling and silent males of the field cricket Teleogryllus oceanicus. *Ecol. entomol.* **20**: 380–383.

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EFFECT OF HABITAT QUALITY ON THE HUNTING BEHAVIOUR OF BREEDING GREAT GREY SHRIKES (LANIUS EXCUBITOR)

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Hunting behaviour and use of different habitat types of a breeding Great Grey Shrike family was observed in a recycled landfill near Eilat, Israel. As Great Grey Shrikes were not observed to breed in the Eilat area for more than a decade, detailed observations of hunting site selection were conducted. Additionally, arthropod abundance and impaled prey items were monitored. The breeding pair established its territory on the boundary of the "Bird Sanctuary", a former recycled landfill, where irrigation has facilitated the growth of dense vegetation inside the park boundary, while outside of it the sparse vegetation characteristic of semideserts is found. Huntings were categorised as either inside or outside of the Bird Sanctuary. White-water traps were applied to measure insect availability inside and outside the Bird Sanctuary. We found that the shrikes foraged preferentially within the Bird Sanctuary (Paired t-test, N=150, t-value: 3.63, P< 0.005). Diversity (revealed by Rényi diversity index) and abundance of arthropods were considerably higher inside the Bird Sanctuary (Wilcoxon Matched-pairs Signed-ranks test, z-value > –2.428, P = 0.0152). The monitoring of impaled prey items revealed that besides insects vertebrates were also taken. Interestingly two specimens of the poisonous Black Cone-headed Grasshopper (*Poikylocerus bufonicus)* were also impaled and consumed.

Key words: Great-Grey Shrike, *Lanius excubitor*, habitat-choice, prey-availability, impaling

INTRODUCTION

Shrikes (Family Laniidae) are prominent birds of open habitats and are important as indicator species of environmental degradation because they are predatory and closely associated with agricultural areas (HANDS *et al.* 1989, SAFRIEL 1995). Shrikes are at present of special concern because many of the 30 species are declining, or have become locally extinct (TUCKER *et al.* 1994, YOSEF 1994). Most long-term studies of previously robust populations of shrikes have documented drastic declines, mostly in the late 20th century (e.g., BUSSE 1995, PEAKALL 1995, PETERJOHN & SAUER 1995).

Several factors have been suggested as causes for shrike population declines, but changes in human land-use practices may be the most likely explanation (e.g., Great Grey Shrike, *Lanius excubitor*, in Switzerland – BASSIN 1981; Red-backed

Shrike, *L. collurio*, in Sweden – OLSSON 1995; Loggerhead Shrike, *L. ludovicianus*, in North America – DROEGE & SAUER 1990; Brown Shrike, *L. cristatus*, in Japan – HAAS & OGAWA 1995). Other explanations range from climate change, i.e., wetter, cooler summers, which reduce activity and abundance of invertebrates (DURANGO 1950, PEAKALL 1962, LEFRANC 1993), to heavy application of inorganic nitrogen fertilisers causing vegetation to grow early, dense and high (ELLENBERG 1986, MARECHAL 1993).

The Great Grey Shrike is extremely widely distributed in the Holarctic region (PANOW 1996), and its breeding area stretches from the North of Europe down to Israel and Northern Africa. The Great Grey Shrike was a common breeding species in the Eilat region (YOSEF 1998) and was extirpated because of rural and housing development and use of biochemicals in the surrounding agricultural fields. Thus, the fact that after a lapse of almost ten years a pair of Great Grey Shrikes established a breeding territory on an area recycled from a garbage dump into a "Bird Sanctuary" by the International Birding and Research Center in Eilat (IBRCE) suggested that the area had become a sustainable habitat for this indicator species.

Optimal foraging theory and the marginal value theorem are widely applied to test how organisms choose feeding sites and prey types based on their profitability (CHARNOV 1976). This predicts that an organism should forage in a patch only so long as the average food intake in this patch is higher than in all other surrounding patches. The combination of prey and patch models (STEPHENS & KREBS 1986) further predicts that patches of highest intake rates are preferred by birds when the size of patches guarantees that their depletion is impossible. In order to test whether Great Grey Shrikes forage optimally we wished to establish whether the birds were able to select foraging sites with higher food availability, and hence higher profitability. We hypothesised that wild Great Grey Shrikes are capable of evaluating the productivity of neighbouring habitats and predicted that the studied birds would spend a relatively greater period of time hunting in the habitat that had greater prey abundance, and was thus energetically more profitable. This study also allowed us to evaluate the success of the experiment wherein we created the "Bird Sanctuary" on top of a landfill, in relation to its surrounding areas. We further hypothesised that owing to the irrigation and higher density of plants in the boundaries of the "Bird Sanctuary," we would find a greater density of entomofauna within the boundaries of the Bird Sanctuary in relation to the surrounding areas.

MATERIALS AND METHODS

The International Birding and Research Center in Eilat (IBRCE), out of concern for the welfare of staging migratory bird populations of Eurasia in the Eilat region, initiated the study of the ef-

fects of human land-use changes on avian migrants. To this effect the IBRCE was allocated a 50 ha landfill as a 'land recycling' experiment. The landfill was in use from the early 1950's till the mid 1970's and was the major landfill for the region. This offered us a unique chance to recycle a 'human abused' landscape and to make it environmentally friendly i.e., to convert it into a 'bird sanctuary'. The ultimate goal is to create a sanctuary for migrant species in the fast growing human-built concrete jungle by planting species that fruit or flower during migration seasons. In addition, the municipality and the Mekorot water works allow the use of partially treated sewage water for irrigating the trees and creating a fresh water lake on the site. The irrigation water is extremely rich in organic matter and has allowed the trees an extremely fast growth and flowering rate, and a higher than normal seed production rate.

During spring 1997 a pair of Great Grey Shrikes established a breeding territory on the western boundary of the bird sanctuary (29°33'N, 34°57'E) and built a nest in an *Accacia radianna* tree. Visits of the parents were monitored for 10 consecutive days, between 30th March and 14th April 1997, for a total of 22 hours. Foraging site of the parents was categorised as either inside or outside the boundaries of the "Bird Sanctuary".

To compare the prey available to shrikes within and outside the bird sanctuary, insect transects and arthropod trapping was conducted in these areas. The length of each invertebrate transect was 50 metres. We recorded all invertebrate seen on the ground or on the vegetation within a 1 m radius of the path (50 × 2 metres). Two transects were conducted, one inside the "bird sanctuary," and one 40 m parallel to the western boundary. The procedure was repeated at an additional locality within and outside the "bird sanctuary." All transects were conducted on 28th April 1997.

The arthropod fauna composition of the habitats was evaluated with the use of white-water traps (HARPER & STORY 1962, SOUTHWOOD 1966). Sixteen (eight in each habitat) white plastic trays of 20.5 cm diameter, filled with 2 cm of water and 2–3 drops of detergent, were placed in the study areas and were emptied after 24 hours. The two trapping sessions were conducted on 22nd and 28th April 1997.

To analyse the white-water trap data we calculated Shannon-Wiener diversity, evenness and Margalef richness indices (PIELOU 1975). Wilcoxon matched-pairs signed-ranks tests (ZAR 1996) were applied to compare the abundance of specimens in each captured invertebrate orders in a pair-wise manner. Diversity ordering, based on the Rényi formula, was also performed for comparison of species richness (TÓTHMÉRÉSZ 1995, 1997). The Rényi diversity index family is well-known for providing reliable results for communities of all sizes (TÓTHMÉRÉSZ 1995). The NuCoSa 1.0 and DivOrd software packages (TÓTHMÉRÉSZ 1993, 1996, 1997) were applied to conduct the calculation of diversity ordering. SPSS PC (NOURIS) and Statistica programme packages were applied to carry out the tests.

RESULTS

A total of 150 foraging sessions were observed. Of these the majority (103 vs 47) were within the boundary of the "Bird Sanctuary" (Fig. 1) and was significantly higher than the number of forages outside (Wilcoxon Matched-pairs Signed-ranks test, 2-tailed, $Z= -2.5992$, $P< 0.0093$).

The total number of invertebrates counted on transects (27 vs 5; Table 1) and collected in the white-water traps (Table 2) was greater inside the bird sanctuary. Both during the first and second trapping the number of invertebrates caught was

Table 1. Entomofauna observed on invertebrate transects within the "Bird Sanctuary" and outside its boundaries

Species	Outside bird sanctuary	Inside bird sanctuary
Lepidoptera sp.	0	6
Diptera sp.	0	18
Formicidae sp.	5	1
Orthoptera sp.	0	1
Heteroptera sp.	0	1
Total	5	27

considerably higher inside the Bird Sanctuary. The pairwise comparison of number of arthropods in each order proved that abundance is significantly higher inside the Bird Sanctuary (Wilcoxon Matched-pairs Signed-ranks test, 2-tailed, first session: $Z = -2.4286$, $P = 0.0152$, second session: $Z = -2.5205$, $P = 0.0117$)

For the first trapping Rényi diversity index was constantly higher for the traps inside the bird sanctuary than on the outside (Fig. 2A). However, for the second trapping session (Fig. 2B) the two lines intersect such that diversity cannot be ranked. The overall result is that abundance of trapped invertebrates is considerably higher inside the bird sanctuary.

The size distribution of the invertebrates trapped outside and inside the Bird Sanctuary also differed considerably. From the total of 196 insects trapped inside the Bird Sanctuary, 57 (29.1%) were larger than 3 mm and 139 (70.9%) were

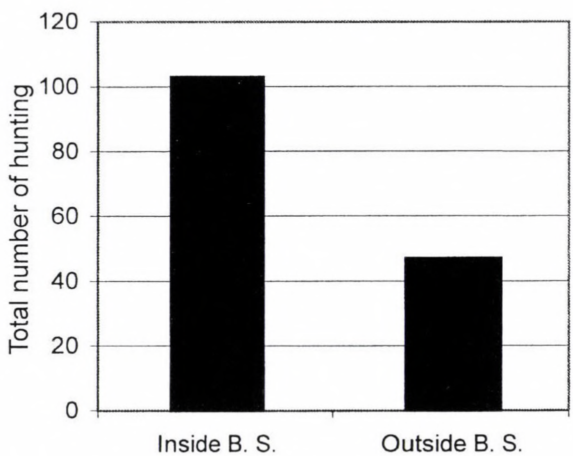


Fig. 1. Proportion of hunting attempts outside and inside the boundaries of the Bird Sanctuary by Great Grey Shrikes. Inside B.S denotes hunting within the boundaries of the Bird Sanctuary; Outside B.S. denotes hunting outside the boundaries of the Bird Sanctuary

smaller than 3 mm. In contrast, outside the Bird Sanctuary from a total of 43 invertebrates, 39 (90.7%) were smaller than 3 mm and only 4 (9.3%) were larger than 3 mm. These proportions of large and small insects were significantly different between the Bird Sanctuary and adjacent areas (χ^2-sqare test, df=1, χ^2=6.25, P=0.0124 after Yates correction).

DISCUSSION

The recycling of a landfill into a bird sanctuary to serve as a staging area for migratory birds is a concept that is not wide-spread. The critical location of Eilat on the eastern flyway of the Palaearctic, and the extensive human development in the region in recent decades, requires such conservation measures to succeed to ensure the continued survival of the Eurasian bird populations. The best possible measure for success is that of the wildlife returning to areas previously abandoned by the species. Unfortunately, the decline or disappearances of bird species from areas where human activities alter habitats are more abundant.

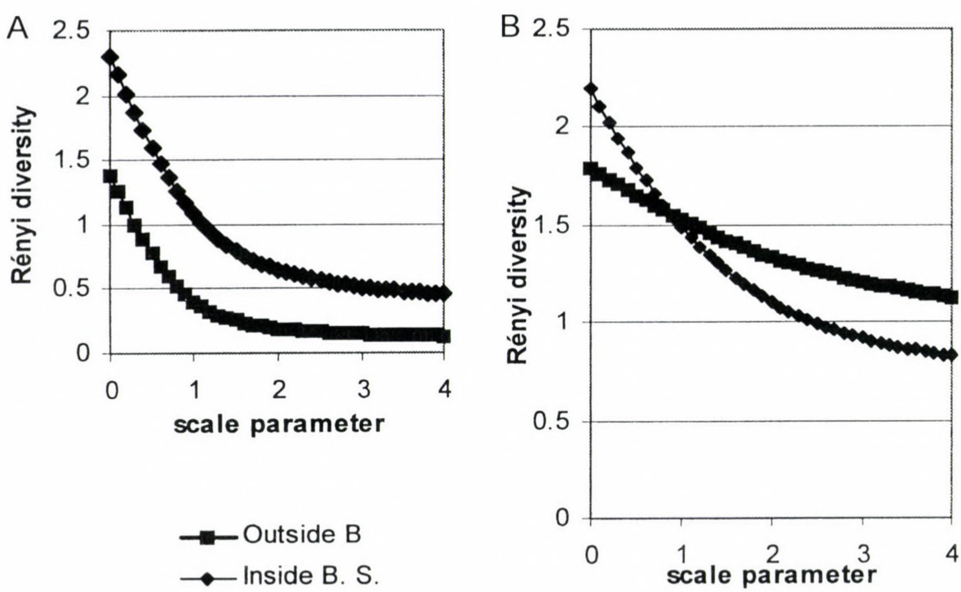


Fig. 2. Rényi diversity ordering for the arthropods caught during the first trapping (A) and second trapping (B). Inside B.S denotes within the boundaries of the Bird Sanctuary; Outside B.S. denotes outside the boundaries of the Bird Sanctuary

Table 2. Results of two sessions of invertebrate trapping using white-water traps inside and outside the boundaries of the "Bird Sanctuary" in Eilat, Israel

Species	21 April		28 April	
	Outside	Inside	Outside	Inside
Hymenoptera	0	15	2	22
Diptera	0	7	14	15
Formicidae	0	22	6	28
Orthoptera	0	1	0	1
Heteroptera	2	1	0	1
Arachnidae	0	3	0	5
Homoptera	0	1	8	16
Coleoptera	1	6	6	6
Lepidoptera	1	1		
Others	39	139	26	109
Total	43	196	62	203
		Diversity		
Shannon index	0.41	1.08	1.52	1.48
		Richness		
Margalef	0.80	1.71	1.21	1.5
Menhinick	0.61	0.71	0.76	0.63

The breeding attempt by the pair of Great Grey Shrikes after an absence of more than a decade in the region is just such an indication. Further, the greater hunting effort calculated for unit observation time was higher in the irrigated area, as was the number of large insects that are suitable for Great Grey Shrikes as prey items. Prey availability is a good predictor of avian foraging decisions, as has previously been proved especially in shrikes (MILLS 1979, YOSEF & GRUBB 1993, 1994). We should also mention that the vegetation inside the Bird Sanctuary provided ample perch-sites, and its importance is highlighted by MOSKÁT *et al.* (2000).

Optimal foraging theory predicts that birds will choose feeding patches, where the average intake rate is the highest, and leave the foraging sites as profitability of other sites is greater due to depletion of prey (SCHOENER 1971, CHARNOV 1973, 1976, PYKE *et al.* 1977). But in reality, large stretches of a given patch, i.e., large areas covered by the same vegetation type, might provide insects or other resources in such quantities that foraging birds can not practically deplete them. STEPHENS and KREBS (1986) formulated a habitat selection prediction for such instances from the patch model and predicted that birds should choose those habitats that provide the highest food intake. For the foraging shrikes different

types of agricultural lands constitute just such habitats (YOSEF & LOHRER 1995, 1998). The study of foraging Loggerhead Shrikes in Florida, U.S.A. (YOSEF & GRUBB 1993) and Red-backed Shrikes (FUISZ 2002) in Hungary, in a habitat, where uncut and cut grass yielded feeding sites with different prey availability showed that more hunting trips were conducted in the patches with uncut grass. The analysis of prey availability in the cut and uncut patches revealed that both the number of large insects and diversity of invertebrates is higher in the patches of uncut grass. Similarly in the case of the Great Grey Shrikes the different types of vegetation inside and outside the boundaries of the Bird Sanctuary maintain different invertebrate communities. The importance of surface dwelling insects in the diet of breeding shrikes was emphasised by several authors (e.g., WAGNER 1994, HROMADA & KRISTIN 1996, SCHÖNN 1995). Both invertebrate-census transects and white-water trapping revealed that abundance of invertebrates was significantly greater inside the recycled landfill and at-present irrigated area. In addition, as the majority of the foraging trips were concentrated inside the Bird Sanctuary, this suggests that the Great Grey Shrike pair foraged optimally, and preferentially, in the given habitat. WHITEHEAD and WRIGHT (1994) also showed that foraging starlings (Sturnus vulgaris) choose meadows that offer a higher food intake.

In our observations in the field, however, we also saw the shrikes hunt actively outside the boundaries of the Bird Sanctuary, in the sparse vegetation. The monitoring of impaled prey revealed that, although during our observations predominantly invertebrate prey were brought to the nest (on one occasion a lizard), the impaled caches consisted predominantly of birds, namely the resident House Sparrow (*P. domesticus)* and migratory Spanish Sparrow (*Passer hispaniolensis*) and Blackcap (*Sylvia atricapilla*). On the mature Accacia trees outside the Bird Sanctuary large flocks of migratory passerine species were frequently observed and appear to be another food source for the breeding shrikes. TYRJANOWSKY *et al.* (1999) also showed in Poland that breeding Great Grey Shrikes preferred and successfully utilised breeding sites containing two different basic habitat types: in the spring crops they hunted for insects and in the adjacent rural meadows they mainly caught vertebrate prey items.

Only two invertebrate specimens were found impaled during our study. Interestingly both were the highly poisonous Black Cone-headed Grasshopper (*Poikylocerus bufonicus).* One of these was consumed three days after impaling and is in contrast to the other impaled vertebrates that were fed to the brood within 24 hours of impaling. The longer period of time probably allowed for detoxification and subsequent consumption of an otherwise unpalatable prey. This has previously been shown to occur in the Loggerhead Shrike (*L. ludovicianus*) that is able to overcome the toxic defenses of a wide range of chemically defended invertebrates,

including lubber grasshopper (*Romalea guttata*), the moth *Utetheisa ornatrix*, and the beetle *Lytta polita*, after "curing" them by impaling for extended periods of time (YOSEF & WHITMAN 1992, YOSEF *et al.* 1996).

All of the above factors combined give a picture of success for the recycled landfill and wherein the environment is in a better balance than the surrounding agricultural or urban areas. Our results support the hypotheses that indeed the Bird Sanctuary has a greater density of entomofauna within the boundaries of the Bird Sanctuary in relation to the surrounding areas, and that Great Grey Shrikes were capable of evaluating the productivity of neighbouring habitats. And consequently the study birds spent a relatively greater period of time hunting in the habitat that had greater prey abundance, and was thus energetically more profitable.

*

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REFERENCES

BASSIN, P. (1981) Répartition et biotopes de la Pie-grièchegrise, Lanius excubitor, dans le nord-ouest de la Suisse (Ajoie, canton du Jura). *Nos Oiseaux* **36**: 1–20.

CHARNOV, E. L. (1973) *Optimal foraging: some theoretical explorations*. Ph.D. diss., Univ. Washington, Seattle.

CHARNOV, E. L. (1976) Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**: 129–136.

DROEGE, S. & SAUER, J. R. (1990) North American Breeding Bird Survey annual summary, 1989. *U.S. Fish Wildl. Serv. Biol. Rep.* **90**: 1–22.

DURANGO, S. (1950) Om klimatets inverkan pa tornskatans (Lanius collurio L.) utbredning och levnadsmojligheter. *Fauna Flora* **45**: 49–78.

DVORAK, M. & ZUNA-KRATHY, T. (1993) Zur aktuellen Situation ausgewahlter Kulturlandvogel im Neusiedlersee-Gebiet. *Vogelkundliche Nachrichten aus Ostosterreich* **4**: 125–138.

ELLENBERG, H. (1986) Warum gehen Neuntöter (Lanius collurio) in Mitteleuropa im bestand zurück? Uberlegungen zu den auswirkungen von pestiziden sowie zu den landschaftsveranderungen im winterquartier und im brutgebiet. *Corax* **12**: 34–46.

FUISZ, T. I. (2002) A tövisszúró gébics (Lanius collurio) fészkelőhely-választását, szaporodási sikerét és térhasználatát befolyásoló tényezők. [Factors influencing the breeding site selection, breeding success and space use of Red-backed Shrikes (Lanius collurio)] In: MTA Emlékbeszédek, felolvasóülések illetve székfoglalók. [In press]

HAAS, C. A. & OGAWA, I. (1995) Population trends of Bull-headed and Brown shrikes in Hokkaido, *Japan. Tech. Publ. West. Found. Vert. Zool.* **6**: 72–75.

HANDS, H. M., DROBNEY, R. D. & RYAN, M. R. (1989) *Status of the Loggerhead Shrike in the northcentral United States*. Unpubl. Rep. U.S. Fish Wildl. Serv., Missouri Coop. Fish Wildl. Res. Unit, Univ. Missouri, Columbia, Missouri.

HARPER, A. M. & STORY, T. P. 1962. Reliability of trapping in determining the emergence and sex ratio of the sugar-beet root maggot Tetanops myopaeformis (Röder) (Diptera: Otitidae). *Can. Ent.* **94**: 268–71.

HOLAN, V. (1993) Populacni hustota a hnizdni bionomie t'uhyka obecneho (Lanius collurio) na Vsetinsku. *Sylvia* **29**: 3–11.

HROMADA, M. & KRISTIN, A. (1996) Changes in the food of the Great Grey Shrike (Lanius excubitor) during the year. *Biologia Bratislava* **3**: 227–233.

JACOBS, J. (1974) Quantitative measurement of food selection. *Oecologia* **14**: 413–417.

JAKOBER, H. & STAUBER, W. (1987) Habitatsansprüche des Neuntöters (Lanius collurio) und massnahmen fur seinem schutz. *Beih. Veroff. Natursch. Landschaft. Bad.-Württ.* **48**: 25–53.

LEFRANC, N. (1979) Contribution a l'ecologie de la Pie-grièche ecorcheur (Lanius collurio L.) dans les Vosges moyennes. *Oiseau* **1**: 245–298.

LEFRANC, N. (1993) *Les Pies-grièches d'Europe, d'Afrique du nord et du moyen-orient*. Delachaux et Niestle, Lausanne. 240 pp.

MALCHEVSKIY, A. S. & PUKINSKIY, Y. B. (1983) *Birds of Leningrad region and adjacent territories*. Leningrad Univ. Press, Leningrad.

MARECHAL, P. (1993) Over externe factoren die de habitatkwaliteit van de Grauwe Klauwier Lanius collurio beinvloeden. *Vogeljaar* **41**: 34–48.

MILLS, G. S. (1979) *Foraging patterns of kestrels and shrikes and their relation to an optimal foraging model.* Ph.D. diss., Univ. Arizona, Tucson.

MOSKÁT, C., FUJIMAKI, Y., YAMAGISHI, S. (2000) Perch site preference of the Bull-headed Shrike (Lanius bucephalus) during the breeding season in Japan. *Ring* **22**(1): 51–57.

OLSSON, V. (1995) The effects of habitat changes on the distribution and population trends of the Great Grey and Red-backed Shrikes in Sweden. *Tech. Publ. West. Found. Vert. Zool.* **6**: 108–111.

PANOW, E. N. (1996) *Die Würger der Paläarktis.* 2nd ed. Magdeburg.

PEAKALL, D. B. (1962) The past and present status of the Red-backed Shrike in Great Britain. *Bird Study* **9**: 198–216.

PEAKALL, D. B. (1995) The decline and fall of the Red-backed Shrike in Britain. *Tech. Publ. West. Found. Vert. Zool.* **6**: 112–116.

PETERJOHN, B. G. & SAUER, J. R. (1995) Population trends of the Loggerhead Shrike from the North American breeding bird survey. *Tech. Publ. West. Found. Vert. Zool.* **6**: 117–121.

PIELOU, E. C. (1975) *Ecological diversity.* Wiley, New York, 159 pp.

PYKE, G. H., PULLIAM, H. R. & CHARNOV, E. L. (1977) Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **4**:137–154.

SCHÖNN, M. (1995) Habitat structure, habitat changes, and causes of decline in the Great Grey Shrike (Lanius excubitor) in southwestern Germany. *Proc. West. Found. Vertebr. Zool.*, 142–149.

SCHOENER, T. W. (1971) Theory of feeding strategies. *Annu. Rev. Ecol. Syst.*, pp. 369–404.

SOUTHWOOD, T. R. E. (1966) *Ecological methods*. Chapman and Hall, London New York.

STEPHENS, D. W. & KREBS, J. R. (1986) *Foraging theory.* Princeton Univ. Press, Princeton, New Jersey.

TÓTHMÉRÉSZ, B. (1993) NuCoSa 1.0: Number cruncher for community studies and other ecological applications. *Abstracta Botanica* **17**: 283–287.

TÓTHMÉRÉSZ, B. (1995) Comparison of different methods for diversity ordering. *J. Vegetation Science* **6**: 283–290.

TÓTHMÉRÉSZ, B. (1996) *NuCoSa: programcsomag botanikai, zoológai és ökológiai vizsgálatokhoz* (Nucosa: software package for botanical, zoological and ecological investigations.) Scientia Kiadó, Budapest, 84 pp.

TÓTHMÉRÉSZ, B. (1997) *Diverzitási rendezések.* (Diversity ordering.) Scientia Kiadó, Budapest, 98 pp.

TUCKER, G. M., HEATH, M. F., TOMIALOJC, L. & GRIMMETT, R. F. A. (1994) *Birds in Europe: their conservation status.* Birdlife Conserv. Series 3. Birdlife Int., Cambridge.

TYRJANOWSKI, P., HROMADA, M. & ANTCZAK, M. (1999) Breeding habitat selection in the Great Grey Shrike Lanius excubitor – the importance of meadows and spring crops. *Acta. Orn.* **34**: 59–63.

WAGNER, T. (1994) Brutzeitliches Beutespektrum des Raubwürgers Lanius excubitor auf Kahlschlag- und Windwurfflache im südwestfalischen Bergland. *Vogelwelt* **115**: 179–184.

WEGGLER, M. (1991) *Brutvogel im Kanton Zürich.* Züricher Vogelschutz, Zürich.

WHITEHEAD, S. C. & WRIGHT, J. (1994) Habitat use by Starlings Sturnus vulgaris flocks: A new method of assessing individual foraging performance. *J. Ornithol.* **135**: 183.

YOSEF, R. (1994) Evaluation of the global decline in the True Shrikes (Family Laniidae). *Auk* 1994: 228–233.

YOSEF, R. (1997) Two decades of studying bird migration at Eilat: a test case of conflicts and paradoxes. *Torgo* **28**: 109–117.

YOSEF, R. & GRUBB, T. C. JR. (1993) Effect of vegetation height on hunting behavior and diet of Loggerhead Shrikes. *Condor* **95**: 127–131.

YOSEF, R. & GRUBB, T. C. JR. (1994) Resource dependence and territory size in Loggerhead Shrikes (Lanius ludovicianus). *Auk* **111**: 465–469.

YOSEF, R. & LOHRER, F. E. (1995) Shrikes (Laniidae) of the world: biology and conservation. *Proc. Western Found. Vertebrate Zool.* **6**: 1–343.

YOSEF, R. & LOHRER, F. E. (1998) Shrikes (Laniidae) of the world: conservation implementation. *Int. Birding and Res. Center, Tech. Publ.* **7**: 1–119.

YOSEF, R., CARREL, J. E. & EISNER, T. (1992) Contrasting reactions of Loggerhead Shrikes to two types of chemically defended insect prey. *J. Chemical Ecol.* **22**: 173–181.

YOSEF, R., LAYNE, J. N. & LOHRER, F. E. (1993) Trends in numbers of Loggerhead Shrikes on roadside censuses in peninsular Florida, 1974–1992. *Fl. Sci.* **8**: 92–97.

YOSEF, R. & WHITMAN, W. (1992) Predator exaptations and defensive adaptations in evolutionary balance: no defence is perfect. *Evol. Ecol.* : 527–536.

ZAR, J. H. (1996) *Biostatistical analysis.* Prentice-Hall International, Inc. 662 pp.

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A REVISION OF THE SPECIES OF PARAMYIA WILLISTON (DIPTERA, MILICHIIDAE) WITH THE DESCRIPTION OF A NEW GENUS

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Species of the widely distributed genus *Paramyia* are revised. Thirteen new species are described: *P. africana* sp. n. (Congo), *P. longilingua* sp. n. (Costa Rica), *P. minuscula* sp. n. (Guyana), *P. regalis* sp. n. (Guyana), *P. setitarsalis* PAPP et SWANN, sp. n. (Guyana, Costa Rica), *P. formosana* sp. n., (Taiwan), *P. flava* sp. n., *P. nitida* sp. n., *P. palpalis* sp. n., *P. Swanni* sp. n., *P. triangularis* sp. n. (Indonesia), *P. latigena* sp. n. (Viet Nam) and *P. flagellomera* sp. n. (Philippines). A key for the World species is given. The genus *Paramyia* is reported from the Afrotropical region and the Asian continent for the first time. The differentiating features of the genus are discussed and a new genus *Paramyioides* (type species: *P. perlucida* sp. n.) is described from Taiwan. With 34 figures.

Key words: *Paramyia, Paramyioides*, new taxa, Milichiidae

The genus *Paramyia* was described by WILLISTON based on a species (*P. nigra* WILLISTON) from the West Indies. At first glance its species are easily recognisable among milichiids by their long proboscis and missing hind cross-vein (dM-Cu) of wing.

Formerly there were only four species known from the Neotropical, Nearctic, Oriental and West Palaearctic regions (see SABROSKY 1965, 1973, 1977, 1989, PAPP 1993). SABROSKY (1965) listed *nitens* (LOEW) from the Nearctic region (with *nigra* WILLISTON as a questionable junior synonym), and he (SABROSKY 1977) listed only *P. inconspicua* DE MEIJERE, 1916 from the Oriental Region. SABROSKY (1989) reported "Unidentified spp." from Australia, Indonesia and some islands. BRAKE (2000) mentioned "P. spp. 2–7" from Borneo, all of them must be new.

The list of the formerly known species is as follows:

Paramyia fumipennis MALLOCH, 1934: 465. Holotype female: Iquitos, Peru (USNM).

Paramyia hungarica L. PAPP, 1993: 135. Holotype male: Aggtelek, Hungary (HNHM).

Paramyia inconspicua DE MEIJERE, 1916: 211. Holotype female: Tjibodas, Java, Indonesia (ZMUA).

Paramyia nigra WILLISTON, 1897: 2. Holotype: Grenada (USNM) (a questionable species, probably a junior synonym of *P. nitens*); unfortunately *P. nigra* WILLISTON is the type species of the genus.
Paramyia nitens (LOEW, 1869): 45 (*Phyllomyza*). Type: Pennsylvania (USNM).

In the collections of the Royal Ontario Museum, Toronto (below: ROM), and of the Hungarian Natural History Museum, Budapest (HNHM) 372 specimens were found. Among them thirteen new species were recognised; these species are described below and a key for the World species is given. Most recently, the author completed a collecting trip to Taiwan, where a new species, representing a new genus, was found, which will also be described.

The type specimens are deposited in the collection of the Royal Ontario Museum (ROM) and in the Department of Zoology of the Hungarian Natural History Museum, Budapest (below HNHM).

Abbreviations used in the text are: *dc*: dorsocentral setae, dM-Cu: distal medio-cubital cross-vein, *ifr*: interfrontal seta, *kepst*: katepisternal seta, *np*: notopleural seta, *ori*: lower fronto-orbital seta, *ors*: upper fronto-orbital seta, *pa*: postalar seta, *poc*: postocellar seta, *pprn*: postpronotal seta, *prsut*: presutural seta, *sa*: supra-alar seta, *sc*: scutellar seta, *vte*: outer vertical seta, *vti*: inner vertical seta, M: medial vein, R: radial veins, R-M: radio-medial cross-vein, S: abdominal sternite, T: abdominal tergite.

Paramyia WILLISTON, 1897

Ocellar (interfrontal) triangle always long, i.e. extended to a shiny (inter)frontal triangle, which in a majority of species reaches to lunule, or in some species even trapezoidal. Postocellars cruciate. One lunular pair of setae. Proboscis (labium with its labella) long to very long. First flagellomere larger than in the related genera, but as for most species, sex-dimorphism in this respect is smaller than in the species of *Phyllomyza*.

Basisternum forming a narrow triangle (this is a shared synapomorphy with *Neophyllomyza*, as revealed by BRAKE (2000)). Thoracic chaetotaxy: 1 *pprn*, 2 *np*, 1 presutural + 1 postsutural intraalar, 1 *pa*, 1 to 3 *dc*, 2 *sc* (laterals vary in length), 1 *kepst* pair of setae. Veins R_{4+5} and M diverging in a majority of the species.

Sternum 1 much reduced (Fig. 7). Male genitalia: Preabdomen of 5 segments. Syntergosternite 6–8 with remains of T6 fused into a more or less symmetrical 5/8 of a ring. Surstylus (Figs 2, 13, 17, etc.) variable, mostly characteristic for species. Distiphallus large, mainly membraneus, "sock-shaped" (BRAKE 2000).

The features of this genus in a sound phylogenetic analysis were revealed by BRAKE (2000) in comparison with all the milichiid genera, particularly with

Xenophyllomyza OZEROV, 1992, *Aldrichiomyza* HENDEL, 1914 and *Neophyllomyza* MELANDER. Before the present revision of the species of *Paramyia* I thought that *Xenophyllomyza* OZEROV, 1992 (type species: *X. deserticola*) described from Turkmenistan is very close or even congeneric with it. I must discard this hypothesis now. Contrarily, by now *Neophyllomyza* seems to be the closest kin. The apomorphic characters for a sister-group relationship between *Paramyia* and *Neophyllomyza* are given by BRAKE (2000).

Indeed, it seems that among the formely known milichiid genera, *Neophyllomyza* is the closest to *Paramyia*. Some of the shared synapomorphies are: proboscis (concretely labium with its labella) very long, first flagellomere large but sex-dimorphism here is not as strong as in *Phyllomyza*, 2 lateroclinate upper fronto-orbital setae. The most conspicuous body characters, which differentiate them even under low magnifications, are as follow:

Paramyia	*Neophyllomyza*
dM-Cu absent	dM-Cu present close to R-M
Frontal triangle distinct, mostly with shiny reflection, in contrast to the rest of frons	frontal triangle tends to be obscure, i.e. not clearly separable from the rest of the frons
Basal tarsomeres with a comb-like row of setae	basal tarsomeres with weak setae

There is one additional medio-reclinate seta between posterior *ors* and *vti*, which was identified as "upper orbital seta" by BRAKE (2000). This seta is not discernible in some species of *Paramyia* and it is always missing in *Neophyllomyza*.

When describing species below, the formerly known species are mentioned first. The descriptions of the new species are given in an alphabetical sequence. Then a new genus *Paramyioides* (type species: *P. perlucida* sp. n.) – with numerous reduced characters, but probably closely related to *Paramyia* – is described from Taiwan.

REVISION OF THE FORMERLY KNOWN SPECIES

Paramyia fumipennis MALLOCH, 1934

Material studied: 1 female (HNHM): Costa Rica, Suiza de Turrialba [on the reverse side] 1921. IV. 21. (The name of the collector of those flies from this locality is not known).

Body length 3.30 mm, wing length 2.87 mm, wing breadth 1.30 mm.

Body and legs shiny black, tarsi dirty yellow.

Frons as long as broad at middle. Face bright shiny, strongly concave, without facial ridge. Labium (without labella) much longer than head. Proboscis very long, total length 1.02 + 1.02 mm. Palpi 0.60 mm, as long as head, with one very strong and several medium-long ventral seta and 4 long apical setae on palpus. First flagellomere larger than in *regalis*, 0.26 mm long, 0.24 mm broad, with a rounded dorsal apex. Gena 0.12 mm broad below eye. Aristal length (0.64 mm) is much more than antennal length (0.41 mm), arista with long hairs (cilia).

Three pairs of *dc*: posterior pair longer than 0.54 mm (apex broken), middle pair 0.36 mm, anterior pair 0.17 mm long. Hind tarsi with a deep ventral ditch and with 9 long ventral setae, second tarsomere more than half as long as basitarsus, with long anteroventral and posteroventral setae.

Wing blackish, on the radial area much darker than on cubital area. Halteres black.

Female cerci thin (only 0.017 mm at widest) and long (0.14 mm) with two pairs of 0.15 mm long apical and several shorter hairs.

Paramyia hungarica L. PAPP, 1993

Holotype male (HNHM): Hungary: A.[ggteleki] N. P., Aggtelek, Medvéskert – cefre csalétek [fermenting fruit bait], 1988. VII. 19., leg. PAPP L.

Measurements in mm: body length 1.26, wing length 1.26, wing breadth 0.578.

Body black and shiny (except for abdomen which is dark grey dusted).

Head higher than long. Ocellar triangle extended to a shiny interfrontal triangle reaching nearly to lunule. Lunule very short, facial keel low and not sharp, mouth edge slightly protruding in profile. Gena half as broad as flagellomere. Both *ors* pairs and both *ori* pairs strong; a short (0.052 mm) additional *ors* between posterior *ors* and *vti; vti* extremely long, *poc* pair long, strong and medioclinate. Flagellomere comparatively long: length/breadth 0.147mm/0.112mm, with long cilia. Arista short, 0.259 mm, its cilia as long as on flagellomere. Whole length of proboscis 0.86 mm. Apex of palpi with 5 straight setae.

Thoracic chaetotaxy: 1 *pprn*, 2 *np*, 1 *prsut*, 1 *sa*, 2 *pa*, 2 *dc*, 1 *prsc*, 2 *sc*. Anterior dorsocentral caudal to supraalar and less than half as long as posterior one. Apical scutellars widely divergent. Proepisternum with a minute seta, anepisternum and anepimeron bare. Katepisternum with 1 very strong *kepst* seta.

Legs brown, short but robust, tarsi light brown. Tarsomeres slightly dorsoventrally flattened. Mid tibia with a strong ventroapical seta, otherwise legs without characteristic setae.

Membrane of wings with some light brownish hue, costal and radial veins greyish ochreous, other veins indistinct yellowish. Cross-vein R-M well proximal to R_1 break of costa. Veins R_{2+3} and R_{4+5} nearly parallel and close to each other. Anal vein distinct on a section of about 0.2 mm as a faint line. Halteres black.

Abdominal terga with dark grey microtomentum. Male genitalia not studied.

Paramyia inconspicua DE MEIJERE, 1916

Holotype female (ZMUA): 1) [hand-written] "Tjibodas, 5000–6000', Koningsberg 1913"; 2)"Paramyia inconspicua" det. de MEIJERE, "Type"; 3) [red, black submargined] TYPE. It is double mounted on a wrinkled silver minuten into a small kerria bricklet.

The holotype female is in a good state of preservation but its right supra- and postalar regions are defected, also right wing displaced, since it was pricked through twice by the minuten pin; left fore leg incl. coxa lost.

Measurements in mm: body length more than 1.25 (abdomen curved down, not precisely measurable), wing length 1.52, wing breadth 0.707.

Mesonotum and abdomen dark brown, subshiny with some greyish microtomentum.

Head higher than long. Anterior third of frons reddish. Frontal triangle reaches ptilinal suture, with greasy shine; lunule not discernible. Facial plate very short, facial keel low, mouth edge strongly protruding in profile. Gena, cheeks and proboscis reddish yellow, genae narrow, only 0.052 mm below eye. Frontal chaetotaxy as usual: both *ors* pairs perpendicularly lateroclinate, both *ori* pairs medioclinate; the short additional *ors* between posterior *ors* and *vti* minute; *vti* extremely long, *poc* pair long, strong, apices crossing. Ocellars as long as the longest fronto-orbital. Two strong peristomals plus several short ones. First flagellomere comparatively short, only ca. 0.085 mm, globular. Arista short though longer than antenna, 0.26 mm, its cilia as long as on flagellomere, i.e. 0.017 mm. Whole length of proboscis 0.31+0.36 mm. Palpi slightly enlarged. Apex of palpi with 3 longer and 3 shorter straight setae.

Thoracic chaetotaxy: 1 *pprn*, 2 *np*, 1 *prsut*, 1 *sa*, 2 (1 extremely long lateral plus 1 short medial) *pa*, 2 *dc* (anterior one more than half as long as posterior one), 1 *prsc*, 2 *sc*. Anterior dorsocentral caudal to supraalar pair. Apical scutellars widely divergent. Proepisternum with a minute bristle, anepisternum and anepimeron bare. Katepisternum with 1 very strong seta.

Legs incl. coxae shiny reddish yellow, short but robust, femora more brownish. Tarsomeres not flattened dorso-ventrally. Mid tibia with a strong 0.10 mm long ventroapical, otherwise legs without characteristic setae. Hind basitarsus rather long (as long as 2nd to 4th tarsomeres combined), ventrally without strong posteroventral or other conspicuous setae.

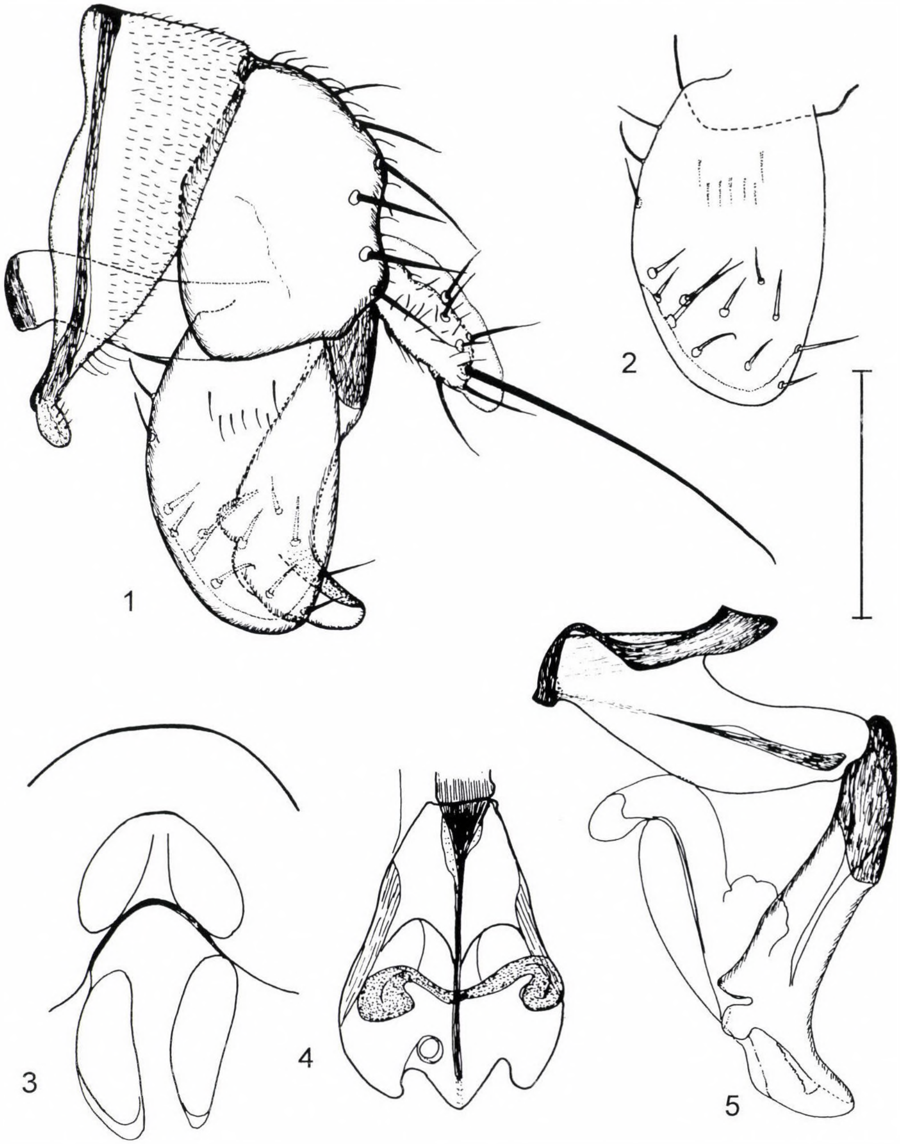
Membrane of wings light brownish, costal and radial veins ochreous, other veins even lighter yellowish. Microtrichia of alar plane comparatively long; stronger costal fringe present to the conjointment of R_{2+3}. Veins R_{2+3} and R_{4+5} nearly parallel and close to each other, slightly divergent apically, third costal section only 0.12 mm. R-M cross-vein slightly proximal to R_1 break of costa. M-Cu and CuA veins very thin. Anal vein distinct on a section of 0.24 mm as a thick, but faint line. Alula narrow. Halteres dark brown.

Abdominal terga with rather long marginal setae. Female genitalia not studied. Cerci long but with moderately long setae only.

Paramyia nitens (LOEW, 1869)
(Figs 1–6)

Material studied (241 specimens): USA, Maine, Malaise traps, 1977, leg. Heinrich (HNHM): 3 males, 5 females: Dryden, 5–8. VIII.; 2 males, 5 females: ibid., 9–14. VIII.; 19 males, 51 females: Strong, 18–24. VII.; 13 males, 25 females: ibid., 24–30. VII. (2 males in microvials with glycerine). 1 male, 1 female (ROM, HNHM): AR, Logan Co., Ozark National Forest, Magazine Mountain, FIT

near intermittent stream, J.E. SWANN, 23. V.–8. VI. 1991. Canada, Ontario (ROM, 2 male and 9 female duplicates in the HNHM): 1 male, 7 females: Gandry Township, Witchdoctor Lake, malaise, 29. viii. 1992, R.A. Cannings & J.E. SWANN; 6 male, 34 females: Hilton Township, malaise at edge of hardwood forest & field, 1992, Leg. J.E. SWANN, from 26.vii. to 13.ix. 2 males, 54 females: Tenby



Figs 1–5. *Paramyia nitens* (LOEW), male genitalia: 1 = syntergosternite and genitalia, lateral view, 2 = surstylus, medial view, 3 = subepandrial sclerites, ventral (inner) view, 4 = hypandrial complex with phallobase, dorsal view, 5 = hypandrial complex and phallus, lateral view. Scale: 0.1 mm for all

Bay, malaise at edge of lakeshore & poplar forest, leg. J.E. SWANN, from 3.viii. to 8.x. 1 female: Hilton Beach, malaise trap, edge of hdwd. for. & field, 25.vii. 90, leg. J.E. SWANN; 1 female: ibid., 18.vii.–2.viii. 87, Hardwood forest, pan traps.

Male first flagellomere enlarged. Labium without labella somewhat longer than head. Palpi shorter than head, with two or more strong ventral setae. Arista as long as antenna. Gena narrower than in *P. hungarica*.

Hind basitarsus with strong ventral setae, but those are not extremely long; also a pecten of short setae present slightly lateral to the strong setae (Fig. 6).

Distance of vein R_{2+3} to costa and to R_{4+5} about the same, i.e. R_{2+3} does not run close to costa.

Male syntergosternite 6–8 with remains of T6 on left lateral side only (Fig. 1). Surstylus (Fig. 2) extremely long. A complex of aedeagal apedeme, hypandrium and gonopods, fused, and joining basiphallus (Fig. 4). Hypandrial arms meet in the sagittal line at the level of their conjointment with epandrium (Fig. 5). Subepandrial sclerites (Fig. 3) comparatively small. Genitalia with distiphallus enormously enlarged. Male cerci (Fig. 1) medially membraneous, apically with a very long seta.

This is the characteristic Nearctic species of the genus. Formerly I thought it to be close to *P. hungarica*, the only Palaearctic species, but the present studies do not support this hypothesis, although they belong to the same species-group.

DESCRIPTION OF THE NEW SPECIES

Paramyia africana sp. n.
(Fig. 10)

Holotype female (HNHM): Congo: Sibiti, Irho [correctly IRHO rain forest], 1–13. XII. 1963., leg. Balogh, Zicsi.

Paratypes: 9 females (two of them without abdomen, HMNM): same as for the holotype. The type specimens are in a rather poor state of preservation. They were minutia-pinned from alcohol (probably from soiled isopropyl-alcohol) numerous years after their capture. Consequently, they are faded and wrinkled; abdomen of two paratypes are lost. The label data are imperfect and in one point, even erroneous. Based on the "Report of the Collectings" by Prof. J. Balogh and his partners, these flies are most probably from the locality numbers of No. 316 to 318. That is, they were captured by soil traps set out on the 1st of December for 5 or 6 days in the plantations of the Institut de Rechèrches pour les Huiles et Oleagineux.

Measurements in mm: body length 1.67 (holotype), 1.54–1.74 (paratypes), wing length 1.69, 1.49–1.72, wing breadth 0.74, 0.67–0.78.

Body brown, mesonotum weakly, abdominal terga thickly microtrichose, i.e. mesonotum and pleura with definite reflection.

Head 0.31 mm long (holotype). Labium (without labella) much longer than head, total length of proboscis 0.465 + 0.50 mm. Palpi slender, as long as head (0.30 mm), with 0.07 mm long subapical and ventral setae, plus 1 very long and 2 shorter apicals. Antenna yellow, first flagellomere 0.085 mm long, 0.12 mm broad. Arista 0. 31 mm, i.e. much longer than antenna (0.17 mm), with long hairs. Gena broad, 0.10 mm below eye, but strongly broadening posteriorad.

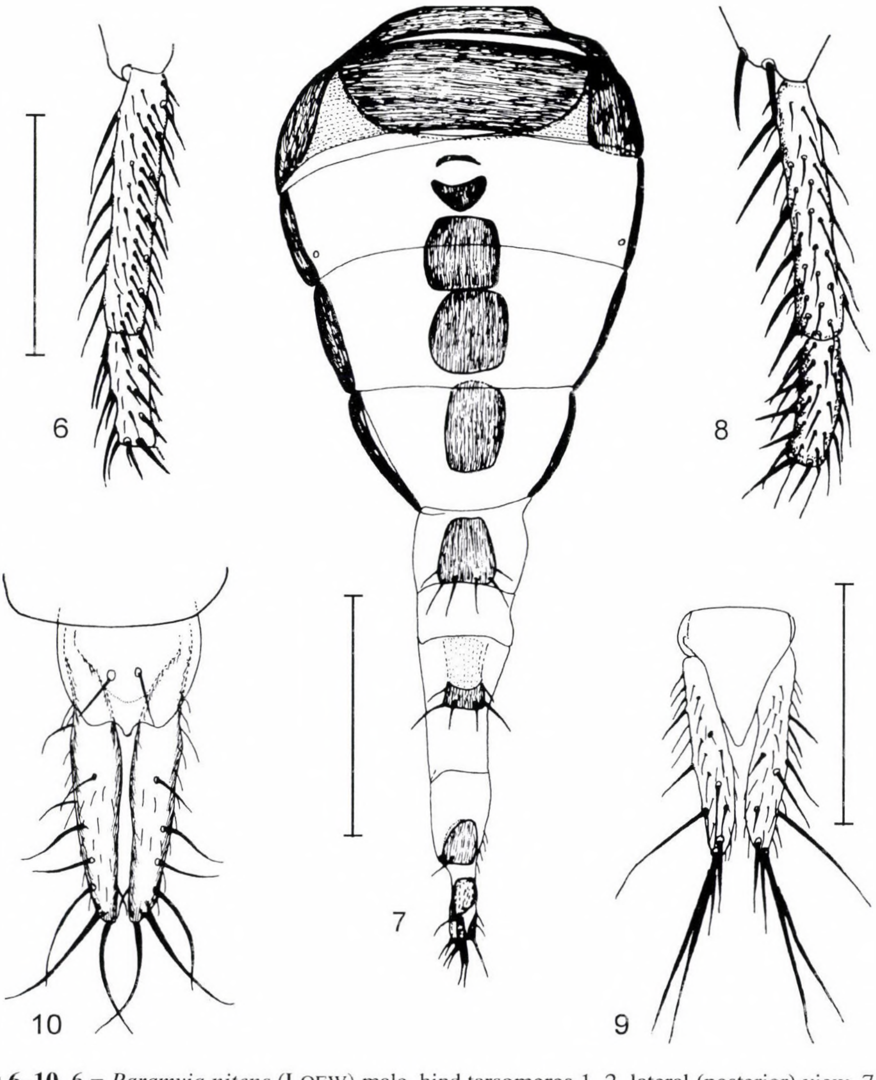
Anterior *dc* comparatively strong, 0.17 mm long, posterior *dc* 0.29 mm, apical scutellars 0.36 mm long. Legs brown, knees and tarsi yellow.

Wings light brown, costal vein ochre. Halteres light brown.

Ventral setae on hind basitarsus particularly strong.

Female cerci comparatively broad, with several medium-long dorsal setae, however apical setae are not very long (Fig. 10). Epiproct is membranous, broader than in *setitarsalis,* hypoproct with a pair of thin setae.

Male unknown.



Figs 6–10. 6 = *Paramyia nitens* (LOEW) male, hind tarsomeres 1–2, lateral (posterior) view. 7–9 = *Paramyia setitarsalis* sp. n., paratype female: 7 = abdomen in ventral view, terminalia in lateral view, 8 = hind tarsomeres 1–2, lateral (anterior) view, 9 = cerci, dorsal view. 10 = *P. africana* sp. n., paratype female, cerci, dorsal view. Scales: 0.4 mm for Fig. 7, 0.2 mm for Figs 6, 8, 0.1 mm for Figs 9–10

This is the only known Afrotropical species of the genus. It is a surprise that it seems closer to the Neotropical species than to the Oriental ones (see key).

Paramyia flagellomera sp. n.
(Figs 11–14)

Holotype male (ROM): Philippines: Negros Oriental: Cuernos de Negros, 7 km W Valencia, 700 m, Malaise w/pans, 8–15. JUL 1987, ROM 873062, DC Darling, E Mayardo. Paratype: 1 male (HNHM, left mid tarsus lost, wings badly wrinkled): Philippines, Leyte: 7 km N. Baybay, Mt. Pangasugan, 250 m, Malaise, 28–30 MAY 1987, ROM 873055, DC Darling.

Measurements in mm: body length 1.60 (holotype), 1.42 (paratype), wing length 1.60, wing breadth 0.62 (wing of paratype not measurable).

Body black, densely grey microtrichose.

Frontal triangle shiny and reaches lunule. Labium without labella as long as head, total length of proboscis (paratype) 0.38 + 0.36 mm. Palpi somewhat shorter than head. Male first flagellomere large, trapezoid-shaped (Fig. 14), i.e. upper apex protruding with a rounded dorsal apex and with rather long hairs. Length/width ratio of the first flagellomere is about 4/5 (0.208 mm vs 0.255 mm on holotype) if length measured dorsally, and about 3/4, if length measured at middle (0.185 mm on holotype, 0.160 vs 0.21 mm on paratype). Pedicel with a long dorsal seta. Arista longer than antenna, so rather long (0.365 mm, 0.382 mm), with long (0.035 mm) hairs. Gena at middle only 0.05 mm broad.

Anterior dorsocentral pair almost half as long as posterior *dc* (0.185 mm and 0.395 mm on holotype). The long *prsc* placed rather cranially, i.e. well anterior to posterior *dc*.

Femora and hind tibia dark brown, fore and mid tibiae and all tarsi dirty yellow. Hind basitarsus not ditched ventrally, with 5 long ventral setae and with a pecten of short dense setae posteroventrally. Halteres dark grey.

Male syntergosternite with larger T6 part ventrally, also spiracles 6 and 7 are rather far from reach other (Fig. 12); the whole syntergostenite covered with microtrichia. Epandrium medium-sized, surstylus comparatively small (Fig. 11), cerci with medium-long setae only. Setae on medial surface of surstylus (Fig. 13) are numerous but not long. Hypandrial complex short but deep (Fig. 11), membranous part of distiphallus not very large.

Etymology. The specific epithet *flagellomera* was given to call attention to the peculiar male first flagellomere.

Paramyia flava sp. n.

Holotype female (ROM): Indonesia: W. Kalimantan, Gunung Palung Nat. Pk., June 17 – June 29 1991, Darling, Rosichon, Sutrisno, IIS 910136 – Cabang Panti Res. Sta. 1°15'S, 110°6'E, 1° rainforest, 100–40 m, Malaise trap (Head), canopy.

Measurements in mm: body length 1.41, wing length 1.41, wing breadth 0.62.

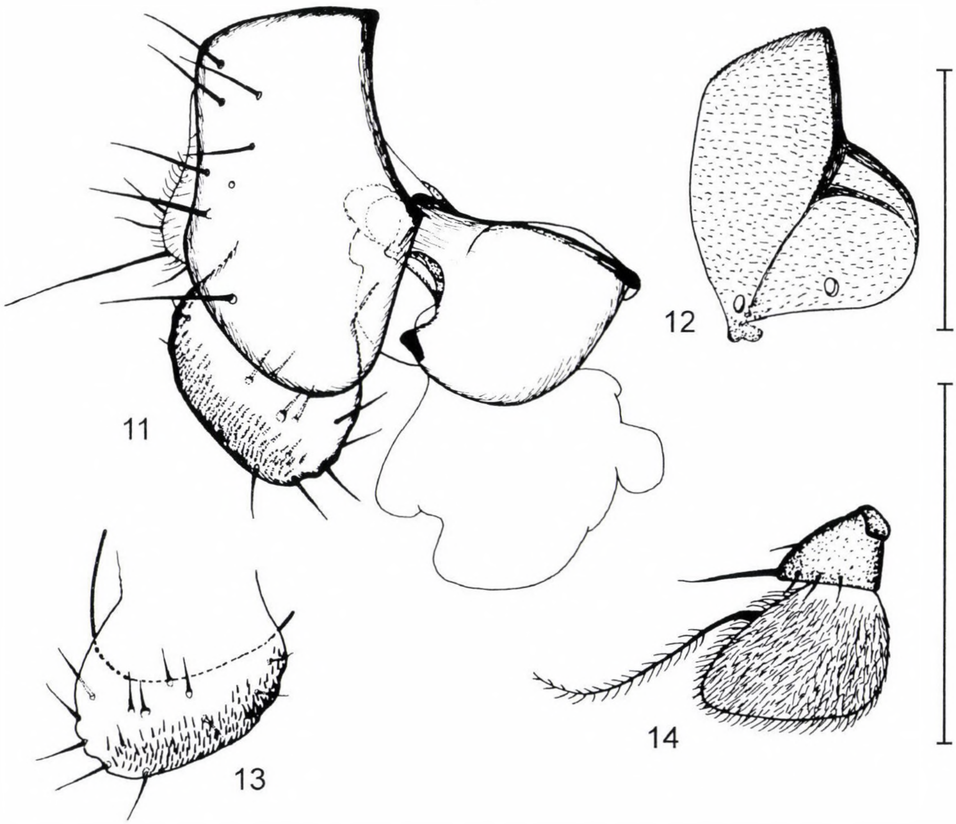
Body and legs mostly yellow with weak reflection, frons brownish, mesonotum yellow with a broad brown stripe between dorsocentrals, both mesonotum and abdomen grey microtrichose, but mesonotum with stronger reflection.

Head 0.28 mm long. Frontal triangle with weak reflection but long and reaches lunule. Gena 0.10 mm broad below eye. First flagellomere black, short globular, as broad as gena (length 0.07 mm, breadth 0.10 mm), pedicel yellow. Proboscis very short (0.21 + 0.21 mm), labium shorter than head. Palpi 0.19 mm, i.e. much shorter than head. Several short or medium-long apical and subapical palpal setae (max. 0.03–0.035 mm). Arista longer than head (much longer than antenna but curved and so not measurable), with short hairs.

Mesonotum slightly depressed dorsally. Anterior *dc* 0.12 mm, posterior pair 0.28 mm long. Also a second supra-alar pair is well discernible. Lateral *sc* comparatively long, 0.21 mm, apical *sc* 0.29–0.30 mm long.

Female cerci 0.09 mm long, with 2 pairs of 0.06 mm long hairs and some short hairs.

Male unknown.



Figs 11–14. *Paramyia flagellomera* sp. n., paratype male. 11 = genitalia, lateral view, 12 = syntergosternite, lateral view, 13 = surstylus, medial (inner) view, 14 = antenna, medial (inner) view. Scales: 0.1 mm for Figs 11–13, 0.5 mm for Fig. 14

P. flava sp. n. is closely related to *P. latigena* sp. n. Although only one and two female specimens are known from these species, body characteristics (see in the key below) seem enough to separate them.

Etymology. The specific epithet *flava* refers to the colour of body.

Paramyia formosana sp. n.
(Figs 15–18)

Holotype male (HNHM): Taiwan: Nantou Hsien, Shuili, forest undergrowth, September 30, 2000, leg. L. PAPP, No. 12. Paratypes: 1 male and 1 female (HNHM): with the same data (most of the female's legs lost).

Measurements in mm: body length 1.80 (holotype), 2.31 (paratype female), wing length 1.92, 2.05, wing breadth 0.78, 0.86.

Body black shiny, abdomen dark grey microtrichose.

Head 0.40 mm long (holotype). Ocellar triangle reaches lunule but apical part narrow, sides concave; triangle shiny with fine longitudinal microscopic striation. Gena 0.085 mm broad below eye. Antenna rather large, first flagellomere 0.145 mm long, 0.19 mm broad (deep), arista as long as head (0.41 mm) or somewhat longer. Labium (without labella) shorter than head, total length of proboscis 0.34 + 0.395 mm. Palpi (0.29 mm) distinctly shorter than head with 2 or more strong ventral setae.

Anterior *dc* 0.16 mm long (holotype), posterior *dc* 0.38 mm long, apical scutellars 0.36 mm.

Ventral setae on hind basitarsus and second tarsomere short (Fig. 15), i.e. shorter than diameter of those tarsomeres. Pecten of short but rather thick setae posteroventrally. Hind second tarsomere shorter or as long as half length of basitarsus.

Wings dark brown, also costal, radial and cubital veins darker brown. Cross-vein R-M well distal to costal break. Anal vein distinct to its distal 4/5 of the virtual length to wing margin. Knob of halteres black, stalk light brown to brown.

Male genitalia (Fig. 16) very characteristic, with short cerci, which bear two pairs of very long and some more long setae. Surstylus (Fig. 17) large, i.e. rather long (see on Fig. 16) and also broad (Fig. 17) with a subbasal medial dentiform projection. Medial surface of surstylus with numerous, rather long setae. Subepandrial sclerites join bases of surstyli (Fig. 18).

Female cerci 0.10 mm long with 2 pairs of 0.085 mm long apical hairs and with several shorter hairs.

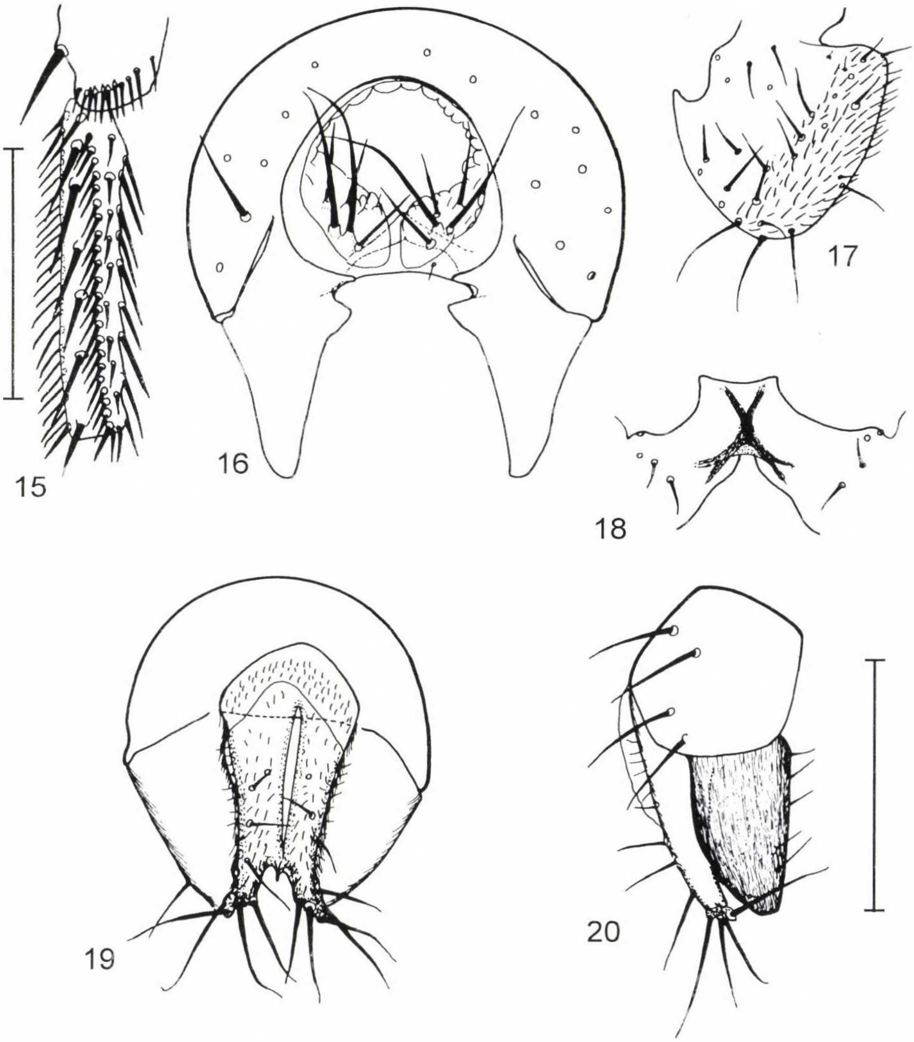
Etymology. The specific epithet *formosana* refers to the old name of the native island, Formosa.

Paramyia latigena sp. n.

Holotype female (HNHM, most of its thoracic setae lost): VIETNAM: Baie d'Ha long, Hông-gai, 0–10 m, l'hôtel, à la lumière, 5. IX. 1963, T. Pócs. Paratype female (HNHM): Vietnam, Cuc phuong, Pr. Ninh binh, 1966. V. 12., leg. Topál.

Measurements in mm: body length 1.47 (holotype), 1.79 (paratype female), wing length 1.67, 1.92, wing breadth 0.65, 0.72.

Frontal triangle, main parts of mesonotum and abdominal terga brown. Face, gena, proboscis, palpi, postpronotum and notopleura as well as legs yellow (paratype discoloured having been kept in alcohol for more than a decade).



Figs 15–20. 15–18 = *Paramyia formosana* sp. n., paratype male: 15 = hind basal tarsomere, submedial view, 16 = epandrium, surstyli and cerci, caudal view, 17 = surstylus, medial (inner) view, 18 = subepandrial sclerite with bases of surstyli, ventral view. 19–20 = *P. minuscula* sp. n., paratype male, genitalia: 19 = caudal view, 20 = lateral view. Scales: 0.2 mm for Fig. 15, 0.1 mm Figs 16–20

Head 0.33 mm long (holotype). Frontal triangle shiny, narrow and short, it terminates far from lunule, reaches only apical 3/5 of frons. Ocellar area darker. Gena 0.11 mm broad below eye. First flagellomere yellowish in its ventral half (brown dorsally), larger than in *flava*, subquadrate, much broader than gena (0.135 mm vs 0.11 mm), length 0.12 mm. Proboscis longer than that of *flava*, i.e. labium (without labella) as long as head; total length of proboscis (holotype) 0.34 + 0.36 mm. Palpi 0.28 mm long, i.e. shorter than head. Arista 0.34 mm on holotype, with short hairs.

Mesonotum shiny. Apical scutellars 0.31 mm (paratype). Hind basitarsus with short ventral setae only, posteroventrally with a pecten of short dense yellow setulae.

Wings light brownish. Cross-vein R-M at the level of R_1 costal break.

Female genitalia not studied; cerci narrow and medium-long with 2 pairs of medium-long but rather thick apical hairs.

Male unknown.

Etymology. This species is named after its extremely wide gena.

Paramyia longilingua sp. n.

Holotype female (HNHM, pinned on a cactal spinule): Costa Rica, Suiza de Turrialba [on the reverse side] 1921. IV. 19. (vibrissal area damaged, flagellomeres, left mid leg and some apical tarsomeres lost).

Measurements in mm: body length 1.11, wing length 1.15, wing breadth 0.59.

Body and even femora shiny black, abdomen with some fine grey microtomentum.

Face protruding well before apical edge of frons ("mouth edge strongly protruding in profile"), length of head measured from apex of face to occiput 0.29 mm, if measured dorsally 0.24 mm. Ocellar triangle extended to a shiny interfrontal trapezoid, sides reaching lunule before meeting each other. Lunule not distinct, facial keel not high or sharp. Gena narrow (0.03 mm below eye). Head setae – compared to the minute body size – rather long, *poc* pair particularly long. Flagellomere lost on the holotype. Whole length of proboscis 0.41 mm + 0.45 mm.

Thoracic chaetotaxy as in its congeners. Anterior dorsocentral distinct, 0.07 mm long, posterior *dc* 0.26 mm. Apical scutellars widely divergent, 0.29 mm long.

Legs black, short but robust, tarsi yellow. Hind basitarsus dorso-ventrally flattened with 5 long ventral setae.

Wings comparatively broad. Membrane of wings clear, costal and radial veins ochre, other veins indistinctly yellowish. Anal vein distinct on its 2/3 of its virtual length to the wing margin. Veins R_{2+3} and R_{4+5} nearly parallel and not close to each other. R_{4+5} straight apically, i.e. completely different from that of *P. minuscula*. Halteres black.

Abdominal terga with very fine grey microtomentum only. Female cerci short (0.03 mm), its longest hairs are longer (0.05 mm) than cerci themselves.

Male unknown.

Etymology. This species is named after its extremely long proboscis.

Paramyia minuscula sp. n.
(Figs 19–20)

Holotype male (ROM): Guyana: Rupununi Dist., 200', Kurupukari, E. side Essequibo R. Savannah scrub/ 1° rainforest edge. malaise. 11–16.X.1990, ROM 905060, B. Hubley, L.D. Coote. Paratypes: 4 males 13 females (ROM, 1 male, 3 females HNHM): Guyana, 1990: 3 males, 2 females: same as for holotype; 1 male, 2 females: ibid., 7–11. x., ROM 905049; 3 females: ibid., 1° rainforest edge/ field, Malaise, 11–16.x., ROM 905057; 2 females: ibid., savannah scrub/ 1° rainforest edge, ROM 905059; 1 female: Mazaruni – Potaro Dist., Tukeit Cr., on E. side Potaro R. downstream Tukeit Falls, 1° rainforest, malaise coarse, 26–30.ix., ROM 905019, B Hubley, LD Coote; 1 female: ibid., malaise-fine, ROM 905020; 2 females: ibid., W. side Potaro R., downstream Tukeit Falls 300', 1° rainforest clearing, Malaise-fine, 27–30.ix., ROM 905025.

Measurements in mm: body length 0.90 (holotype), 0.88–0.99 (paratype males), 1.17–1.48 (paratype females), wing length 0.89 (holotype), 0.86–0.98 (paratype males), 1.06–1.47 (paratype females), wing breadth 0.38 (holotype), 0.38–0.42 (paratype males), 0.43–0.64 (paratype females).

Body shiny black.

Head somewhat higher than long. Ocellar triangle large, apex reaches lunule, with silky reflection (i.e. not shiny), frontal triangle surrounded by 6 pairs of comparatively short ifr. Face short, much protruding ventrally, facial keel inconspicuous. Clypeus very thin. Both *vte* and *vti* pairs very long, orbital setae not so much; *poc* pair long. Male first flagellomere rather large (0.08 mm long, 0.11 mm broad (deep)), arista somewhat longer than antenna, its cilia short. Whole length of proboscis 0.20 + 0.22 mm, labium without labella as long as head. Palpi shorter than head, apex of palpi with 5 or more short setae. Also vibrissa and peristomals weak. Gena narrow, 0.025 mm below eye.

Anterior dorsocentral hardly longer than L' of posterior one. Prescutellar pair short. Apical scutellars no strongly divergent. Katepisternum with 1 very strong bristle (compared to the body size).

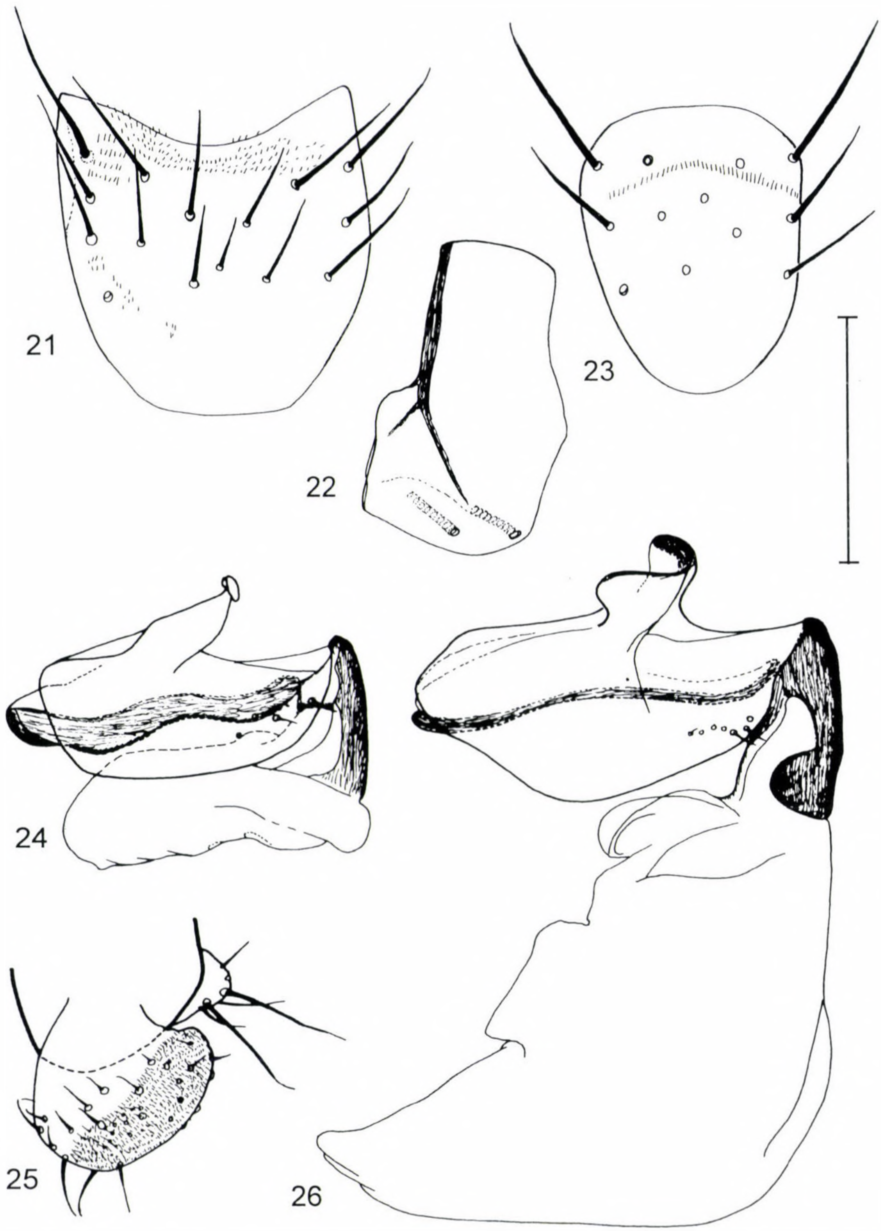
Legs brown, short but robust, knees, apices of tibiae and tarsi light brown. Tarsomeres short in general. Hind basitarsus without long setae but with a row of medium-long setae and with a pecten of short setae.

Membrane of wings clear, costa and radial veins R_1 and R_{4+5} ochre, R_{2+3} colourless, other veins indistinct. Vein R_{4+5} slightly upcurved at apex, terminating far from the apex of wing. At the level of apical fourth of wing, cells r_1 and r_{2+3} combined are narrower than cell r_{4+5}. Anal vein discernible at its basis only. Stalk of halteres black, knob light brownish.

Abdominal terga with fine greyish microtomentum.

Male genitalia (Figs 19–20) very characteristic: epandrium small, though rather broad in posterior view (Fig. 19). Cerci extremely large, long, well-sclerotized apically with a lateral process, the apical part bears five long setae. Surstyli (Figs 19–20) also very large, longer than length or height of epandrium, subtriangular in lateral view.

Etymology: from the Latin word "*minuscula*" = very small.



Figs 21–26. 21–22 = *Paramyia nitida* sp. n., paratype male: 21 = sternum 5 ventral view, 22 = syntergosternite, lateral view; 23–25 = *P. palpalis* sp. n., male: 23 = sternum 5, ventral view, 24 = hypandrial complex, lateral view, 25 = surstylus, medial (inner) view; 26 = *P. nitida* sp. n., paratype male, hypandrial complex, lateral view. Scale: 0.1 mm for all

Paramyia nitida sp. n.
(Figs 21–22, 26–27)

Holotype male (ROM): Indonesia: Sumatra, Aceh: Mt. Leuser Natl. Pk., Ketambe Res. Stn. 5 SEP 1989, ROM 893036, B. Hubley – lowland rainforest, screen sweep, 350 m, young forest (T3), riparian vegetation. Paratypes: 5 males, 3 females (ROM, 2 m, 1 f HNHM): 1 male (wings and all – but right mid – legs lost), 2 females: same as for holotype; 1 male, 1 female: ibid., 3–8 SEP, ROM 893045; 1 male: ibid., 7 SEP, ROM 893059, DC Darling, mature forest (T4), light gap; 1 male: ibid., 9–21 SEP, DC Darling – Malaise w/pans, mature forest (T4), light gap, 350 m.

Measurements in mm: body length 1.58 (holotype), 1.36–1.60 (paratype males), 1.78–2.05 (paratype females), wing length 1.48 (holotype), 1.30–1.48 (paratype males), 1.58–1.83 (paratype females), wing breadth 0.62 (holotype), 0.53–0.62 (paratype males), 0.67–0.80 (paratype females).

Body black shiny, femora also with strong reflection.

Frontal triangle large (nearly reaching lunule), shiny, with some fine longitudinal microscopic striation. Labium without labella as long as head, total length of proboscis 0.33 + 0.36 mm (holotype). Palpi shorter than head. Ventral palpal setae are shorter than palpal diameter at their base. Male first flagellomere 0.135 mm long, 0.173 mm broad (deep). Arista 0.40–0.41 mm (holotype), i.e. longer than antenna, with medium-long hairs.

Anterior *dc* 0.12 mm (holotype), posterior *dc* 0.34 mm, apical scutellar setae 0.37 mm long. Femora and hind tarsi dark brown, fore tibia, fore and mid knees and all tarsi dirty yellow, mid tibia brown. Hind basitarsus with 6 (5) very long setae ventrally in a shallow ditch, also setae in the posteroventral pecten longer than in *flagellomera* or *Swanni*. Second tarsomere with 5 (4) pairs of long anteroventral and posteroventral setae. Halteres dark brownish grey.

Male sternum 5 (Fig. 21) broad with rather numerous long setae, which are somewhat shorter than those of *P. palpalis* though (cf. Fig. 23). Syntergosternite (Fig. 22) comparatively long, particularly so ventrally, spiracles 6 and 7 rather far from each other. Surstylus (Fig. 27) rather large, very broad basally and widely rounded apically but with a definite basal-caudal corner. Medial surface of surstylus with almost evenly distributed medium-long setae; caudal microtrichose area rather large (Fig. 27). Membranous part of distiphallus (Fig. 26) enormously large, comparatively largest among the *Paramyia* species known to me.

Etymology. The specific epithet *nitida* is to express the conspicuous shine of its body (compared to its relatives).

Paramyia palpalis sp. n.
(Figs 23–25)

Holotype male (ROM): Indonesia: W. Kalimantan, Gunung Palung Nat. Pk., June 15 – August 15, 1991, Darling, Rosichon, Sutrisno, IIS 910116 – Cabang Panti Res. Sta. 1°15'S, 110°5'E, 1° rainforest, Malaise trap head, Sandstone – light gap. Paratypes: 1 male, 3 females (ROM, 1 male and 1 female HNHM): same as for the holotype, 5 females (ROM, 1 HNHM): ibid., IIS 910119, Sandstone-closed. The paratype male is in a poor state of preservation: its right flagellomere, both aristae and most of the legs are lost.

Measurements in mm: body length 1.54 (holotype), 1.45 (paratype male), 1.63–2.12 (paratype females), wing length 1.54 (holotype), 1.482 (paratype male), 1.53–1.90 (paratype females), wing breadth 0.67 (holotype), 0.62 (paratype male), 0.68–0.78 (paratype females).

Body black, less shiny than body of *P. nitida*.

Head 0.32, 0.34 mm long (paratype and holotype males). Frontal triangle large and shiny, with fine longitudinal microscopic striation. Labium without labella as long as head, total length on the holotype 0.32 + 0.34 mm. Palpi shorter than head, but their setae are rather long: ventral palpal setae longer than the diameter of palpus at their base. Male antenna large, length 0.155 mm (holotype), 0.16 mm (paratype), breadth (depth) 0.180, 0.185 mm. Arista longer than antenna (0.38 mm on holotype) with long hairs.

Anterior *dc* thick, 0.16 mm (holotype), posterior *dc* 0.38 mm, apical scutellar setae 0.41 mm long. Femora and hind tibia dark brown, fore and mid knees and tibiae, and all tarsi dull yellow. Hind basitarsus with a ventral ditch, with 5 long ventral setae (up to 7 on large females), setae in the posteroventral pecten particularly strong, similarly to those of *P. nitida*.

Male S5 narrower than that of *P. nitida*, with less but longer setae (Fig. 23). Surstylus rather large (Fig. 25), apical part semicircular, basal-caudal part rounded (edged in *nitida*). Male distiphallus (Fig. 24) though large, much smaller than that of *nitida* (Fig. 24).

Female cerci (measured on largest female) 0.10 mm long, only 0.018 mm broad, longest hairs 0.085 mm.

Etymology. The specific epithet was given to call attention to its ventral palpal setae, which are longer than diameter of palpus at their base.

Paramyia regalis sp. n.

Holotype female (ROM): Guyana: Rupununi Dist., Kurupukari, Essequibo R., 200', malaise, 1° rainforest, clearing, 7–11.x.1990, ROM 905048, L.D. Coote & B. Hubley. Paratype female (HNHM): ibid., W. side Essequibo R. 1° rainforest, malaise, 8–16.x.1990, ROM 905064, B Hubley.

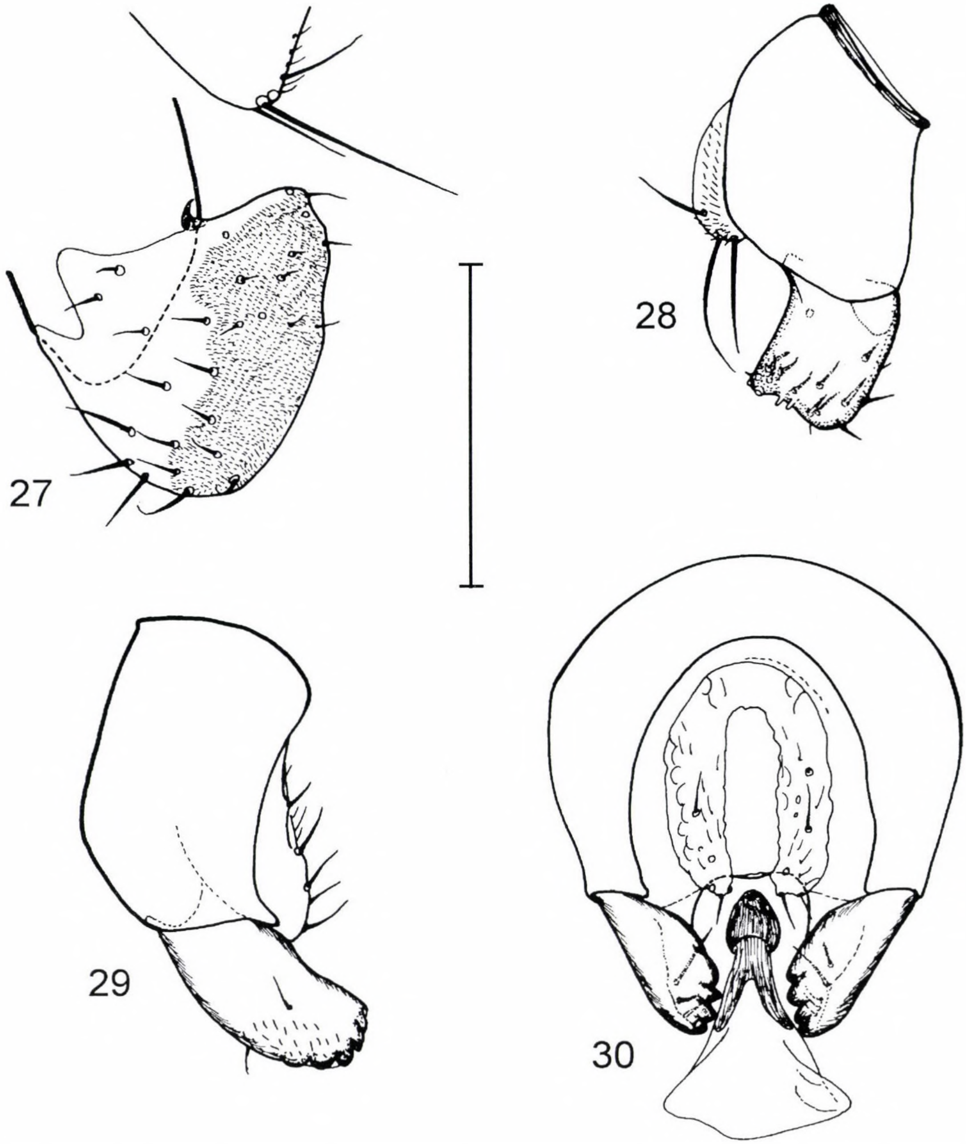
Measurements in mm: body length 2.25 (holotype female), 2.37 (paratype), wing length 2.18, 2.20, wing breadth 0.90, 0.93.

Body shiny black, particularly on pleura, abdomen with fine microtomentum, so almost as shiny as thorax.

Head with frons longer than its breadth at middle. Frontal triangle shiny, slightly trapezoid, i.e. both sides meet lunular opening before meeting each other. Head setae extremely long, also occipital setae rather large. Anterior *ori* anterior to cranial edge of frons, anterior margin of frons with 2 pairs of long setae (medial pair belongs to *ifr*). Five pairs of *ifr*. Labium (without labella) much longer than head, though proboscis as a whole shorter than in *fumipennis*. Total length of proboscis 0.74 + 0.83 mm. Palpi large, as long as head or even longer, one very strong ventral seta and 4 shorter but still strong setae, which are placed almost symmetrically around apex of palpus. First flagellomere subquadrate, 0.17 mm long, 0.20 mm broad (deep). Arista much longer than whole antenna, with 0.025 mm long hairs (cilia). Gena 0.086 mm broad below eye.

Three pairs of dorsocentrals: posterior pair 0.53 mm, middle pair 0.285 mm, anterior pair 0.123 mm long. Apical scutellars widely divergent, 0.63 mm long.

Legs dark brown, tarsi yellow. Hind basitarsus with a deep ditch in its whole length, surrounded by 6 extremely long setae anteriorly and by a pecten of dense short stiff parallel setae poteriorly; 2nd tarsomere with 4 pairs of very long anteroventral and posteroventral setae.



Figs 27–30. *Paramyia* spp. n., male genitalia. 27 = *P. nitida* sp. n., paratype, surstylus with apex of cercus, medial (inner) view; 28 = *P. swanni* sp. n., holotype, epandrium, surstylus and cercus, lateral view; 29–30 = *P. triangularis* sp. n., paratype: 29 = lateral view, 30 = caudal view. Scale: 0.1 mm for all

All wing veins yellow and well expressed (discernible). Anal vein discernible to ca. 4/5 of its virtual length to wing margin. Halteres black.

Female cerci comparatively short, with short (max. 0.10 mm) hairs.

Etymology. The specific epithet *regalis* (the Latin word for "royal" or "king-like") refers to the impressive outlook (habitus) of this species.

Paramyia setitarsalis PAPP et SWANN, sp. n. (Figs 7–9)

Holotype female (ROM): Guyana: Rupununi Dist. 200', Kurupukari, E. side Essequibo R. 1° rainforest edge/field, malaise. 7–11.X.1990, ROM 905050, B Hubley, LD Coote.

Paratypes: 60 females (ROM, 8 specimens of the duplicates in HNHM): 6 females: same as for holotype, plus 6 females: same, but ROM 905055; 10 females: ibid., 11–16.X., ROM 905057; 9 females: ibid., savannah scrub/1° rainforest edge, Malaise, 7–11.X., ROM 905049; 2 females: same as 905049, but ROM 905059, 905060; 7 females, ibid., malaise, 1° rainforest clearing, 7–11.X., ROM 905048; 1 female: same as 905048 but 8–16.X., ROM 905058; 3 females: same as 905048 but 11–16.X., ROM 905056; 6 females: ibid., W side Essequibo R., 1° rainforest/cattle trail, Malaise, 8.–16.X., ROM 905063; 1 female: same as 905063 but ROM 905061; 2 females: ibid., 1° rainforest, malaise, 8–16.X., ROM 905064; 4 females: Mazaruni-Potaro Dist., W. side Potaro R. downstream, Tukeit Falls, 300', rainforest clearing, malaise-fine, 27–30.IX., ROM 905025; 1 female: ibid., Tukeit Cr. on E side Potaro R. downstream Tukeit Falls, 300', 1° rainforest, malaise-coarse, 26–30. IX., ROM 905019; 1 female: ibid., E side Potaro R. downstream Tukeit Falls, 300', 1° rainforest edge/scrub, malaise-coarse, 26–30.IX, ROM. 905024; 1 female: as 905024, but 1° rainforest dry streambed, malaise-coarse, ROM 905022. 1 female (HNHM, pinned on a cactal spinule): Costa Rica, Suiza de Turrialba [on the reverse side] "1921. V. 1".

Measurements in mm: body length 1.67 (holotype), 1.29–1.71 (paratypes), wing length 1.44 (holotype), 1.22–1.59 (paratypes), wing breadth 0.63 (holotype), 0.53–0.69 (paratypes).

Body dark brown or black, shiny, particularly so for thoracic pleura.

Head 0.31 mm (holotype). Ocellar triangle reaches lunule but apical part rather narrow, i.e. sides are concave. Gena half as broad as first flagellomere (0.06 vs 0.12 mm). Both *ors* pairs and both *ori* pairs strong; a distinct (0.12 mm) additional *ors* between posterior *ors* and *vti; vti* extremely long, *poc* pair long, strong and crossing each other. Length of eye 0.233 mm, genae below eye only 0.052 mm broad (holotype). Flagellomere globular, 0.10 mm long, 0.12 mm broad (deep), with long cilia. Arista much longer than antenna, with long hairs (cilia). Whole length of proboscis 0.50 + 0.55 mm. Palpi as long as head, or slightly shorter (0.26 mm), apex of palpi with 2 very long (0.085 mm) and 2 shorter setae, also a strong 0.10 mm long ventral bristle present.

Anterior dorsocentral caudal to supraalar and more than half as long as posterior one (0.21 mm vs 0.36 mm). Apical scutellars 0.595 mm, widely divergent, basal pair 0.21 mm long (holotype). Katepisternal seta very strong.

Legs dark brown, only knees and tarsi yellow. Hind tarsomeres 1 and 2 with extremely long and thick setae (Fig. 8); similarly to the species of Phoridae these setae are equipped with microtrichia. Mid tibia with a strong ventroapical, otherwise legs without characteristic setae.

Membrane of wings quite clear with strong reflection, costal and radial veins ochre, other veins pale yellowish. Veins R_{2+3} and R_{4+5} nearly parallel to each other. Cross-vein R-M well proximal to R_1 break of costa. Halteres waxy yellow.

Abdominal terga with dark grey microtomentum. Sternum 2 small and all the sterna are narrow. Sternum 8 small but distinct, not divided. Epiproct membranous, cerci long and narrow, apically with 2 pairs of very long setae (Fig. 9), apical third of cerci also with some more long setae.

Male unknown.

Etymology. This species is named after the extremely long setae on its hind basitarsus.

Paramyia swanni sp. n. (Fig. 28)

Holotype female (ROM): Indonesia: Sumatra, Aceh Prov.: Mt. Leuser Natl. Pk., Ketambe Res. Stat., 350 m, malaise head, young forest, closed canopy, 3–10.ix.1989, ROM 893027, B. Hubley, D.C. Darling. Paratype female (HNHM): same as for holotype.

Measurements in mm: body length 1.185 (holotype male), 1.35 (paratype female), wing length 1.16, 1.37, wing breadth 0.40, 0.54.

Body dark greyish brown, subshiny, mesonotal microtrichia give a greasy reflection.

Frontal triangle large, with silky reflection (i.e. not strongly shiny). Head setae not very long. Male first flagellomere large quadrate, but not trapezoid (as in *flagellomera*), length equals breadth, 0.125 mm (female first flagellomere much smaller, globular). Arista 0.28–0.30 mm long with medium-long cilia. Labium without labella, shorter than head. Palpi somewhat shorter than head. Gena only 0.04 mm broad.

Posterior dorsocentral pair rather strong (0.26 mm long), anterior pair weak as also in its congeners, only 0.075 mm long. Apical scutellars only slightly divergent and very long (0.28 mm on the holotype, *vs* its 1.185 mm body length).

Wing similar to the related species, i.e. vein R_{4+5} almost straight at apex, terminating very close to the apex of wing. At the level of apical fourth of wing cells r_1 and r_{2+3} combined much wider than cell r_{4+5}. Halteres dark greyish brown.

Legs dark brown, knees and tarsi lighter (ochre). Tarsi short. Male hind basitarsus with 5 medium-long setae ventrally and a posteroventral pecten of short parallel setae. Also second tarsomere with 4 pairs of medium-long setae.

Male genitalia (Fig. 28) rather small. Cercus short with 3 longer setae. Surstylus small quadrate with definite apical-caudal apex and with short to medium-long setae only.

Female postabdominal terga very short. Cerci thin with fine hairs only.

Although *P. swanni* sp. n. keys together with *nitida* and *palpalis*, we think, *P. triangularis* is a closer relative. Their surstylus differ characteristically though.

Etymology. I name this species after Mr John SWANN (Royal Ontario Museum, Toronto) in order to express my gratitude for his help in the introductory phase of this study.

Paramyia triangularis sp. n.
(Figs 29–30)

Holotype male (ROM): Indonesia: Sumatra, Aceh: Mt. Leuser Natl. Pk., Ketambe Res. Sta. 9–21 SEP 1989, ROM 893093, DC Darling – lowland rainforest, Malaise w/pans, mature forest (T4), light gap, 350 m. Paratypes: 1 male, 5 females (ROM, 1 m, 1 f HNHM): 2 females: same as for holotype; 1 male, 1 female: ibid., 5 SEP 1989, ROM 893036, B. Hubley – lowland rainforest, screen sweep, 350 m, young forest (T3), riparian vegetation; 2 females: ibid., 3–8 SEP, ROM 893045, B. Hubley, DC Darling – lowland rainforest, Malaise head, 350 m, mature forest (T4), light gap.

Measurements in mm: body length 1.28 (holotype), 1.09–1.75 (paratype females), wing length 1.27 (holotype), 1.17–1.70, wing breadth 0.53 (holotype), 0.52–0.74.

Body black , mesonotum and abdomen with grey microtomentum.

Frontal triangle large, almost dull, with a slight reflection only. Postocular setae originate far from each other, outside lateral ocelli (contrary to e.g. *P. nitida*).

Male first flagellomere only slightly enlarged, globular: length 0.085 mm, breath (depth) 0.11 mm (holotype). Labium without labella, somewhat shorter than head. Total length of proboscis 0.22 + 0.235 mm (holotype). Palpi shorter than head, slightly swollen supapically, rounded apically, with 1 thick ventral and 4–5 apical-subapical medium-long but thick setae. Arista longer than antenna (0.42–0.43 mm on holotype), with long (ca. 0.025 mm) cilia.

Anterior *dc* of holotype 0.11 mm, posterior dc 0.31 mm, apical scutellar pair 0.36 mm long. Legs dark brown, at most mid and hind tarsi somewhat lighter. Hind basitarsus with 5–6 long setae and a pecten of short parallel setae.

Male epandrium short but rather high (Fig. 29), cerci not small, rather high but bear only comparatively short setae. Surstylus (Figs 29–30) long, slightly curved ventro-caudally, apically with 4 small lobes (which is unique among the *Paramyia* species hitherto known). Surstylus only sparsely setose. Distiphallus comparatively small (Fig. 30).

Female cerci comparatively short, with short hairs only (max. 0.05 mm).

Etymology. The specific epithet refers to the large frontal triangle of this species.

KEY TO THE WORLD SPECIES OF PARAMYIA WILLISTON, 1897

1 (2) Proboscis almost as long as body, labium without labellae 1.5 times as long as head. Frontal triangle trapezoidal. Body length 1.1 mm (Costa Rica) **longilingua** sp. n.

2 (1) Proboscis much shorter than body length. Frontal triangle with an apex anteriorly (slightly trapezoidal in *regalis*).

3 (6) Body yellow or at least partly – i.e. gena and pleurae – yellowish. Gena as wide as pedicel (Oriental Region).

4 (5) Frontal triangle short and shiny, terminates far from lunule. Female first flagellomere large, subquadrate, much wider than gena and its ventral half

yellowish. Mesonotum brown, except for postpronotal tubercle and notopleura (Viet Nam). **latigena** sp. n.

5 (4) Frontal triangle with weak reflection only but reaches lunule. Female first flagellomere short, globular and black, only as wide as gena. Mesonotum yellow with a broad brown stripe between dorsocentrals (Indonesia) **flava** sp. n.

6 (3) Body brown or black. Gena much narrower than pedicel.

7 (14) Labium without labella much longer than head. Palpi as long as head. Arista longer or much longer than antenna, with long aristal cilia. Ventral setae on hind basitarsus particularly strong.

8 (11) Larger species (body length 2.25–3.30 mm) with dark wings (Neotropical Region).

9 (10) Wings on the radial area much darker than on cubital area. Frons as long as broad at middle *fumipennis* MALLOCH, 1934

10 (9) Wings evenly dark. Frons longer than its breadth at middle. **regalis** sp. n.

11 (8) Smaller species (body length 1.3–1.75 mm) with clear wings.

12 (13) Frontal triangle bright shiny, i.e. strongly contrasting to the rest of frons. Frontal triangle much narrowed anteriorad, very narrow anteriorly and just reaching lunule (Costa Rica, Guyana) **setitarsalis** sp. n.

13 (12) Frons dull, i.e. shine of frontal triangle not much different from the rest of frons. Frontal triangle evenly narrowed anteriorad (Congo) **africana** sp. n.

14 (7) Labium without labella at most as long as head. Palpi usually shorter than head (in cases when labium is somewhat longer, palpi always shorter than head).

15 (16) Vein R_{4+5} slightly upcurved at apex, terminating far from the apex of wing. At the level of apical fourth of wing cells r_1 and r_{2+3} combined are narrower than cell r_{4+5}. Body length 0.88–1.48 mm (Neotropical) **minuscula** sp. n.

16 (15) Vein R_{4+5} not upcurved at apex, terminating at or not far from the apex of wing. At the level of apical fourth of wing cells r_1 and r_{2+3} combined are wider than cell r_{4+5} (Nearctic or Old World species)

17 (20) Frontal triangle with weak silky or greasy reflection only. Male first flagellomere not enlarged (male not known in *inconspicua*) (Indonesia).

18 (19) Anterior third of frons, cheeks, genae and legs incl. coxae reddish yellow. Smaller, 1.21 mm (Java) *inconspicua* DE MEIJERE, 1916

19 (18) Frons, cheeks, genae and legs black, or at least brown. Mostly larger, up to 1.75 mm (Sumatra) **triangularis** sp. n.

20 (17) Frontal triangle distinctly shiny. Male first flagellomere enlarged.

21 (26) Ventral setae on hind basitarsus and second tarsomere short (Fig. 15), i.e. shorter than diameter of those tarsomeres. Hind second tarsomere shorter or as long as half-length of basitarsus. In cases of bias, labium is definitely longer than head.

22 (23) Larger species, body length 1.8 to 2.3 mm. Wings dark, Palpi with 3 strong ventral setae. Male genitalia as in Figs 16–17 (Taiwan) **formosana** sp. n.

23 (22) Smaller species, body length 1.2 to 1.4 mm. Wings clear. Palpi with only 1, seldom 2 strong ventral setae. Male genitalia are different (e.g. Figs 1–2).

24 (25) Distance of vein R_{2+3} to costa and to R_{4+5} about the same. Male flagellomere much enlarged, almost as long as head and as broad as long (U.S.A., southern Canada, Mexico, West Indies) (? = *nigra* WILLISTON, 1897) *nitens* (LOEW, 1869)

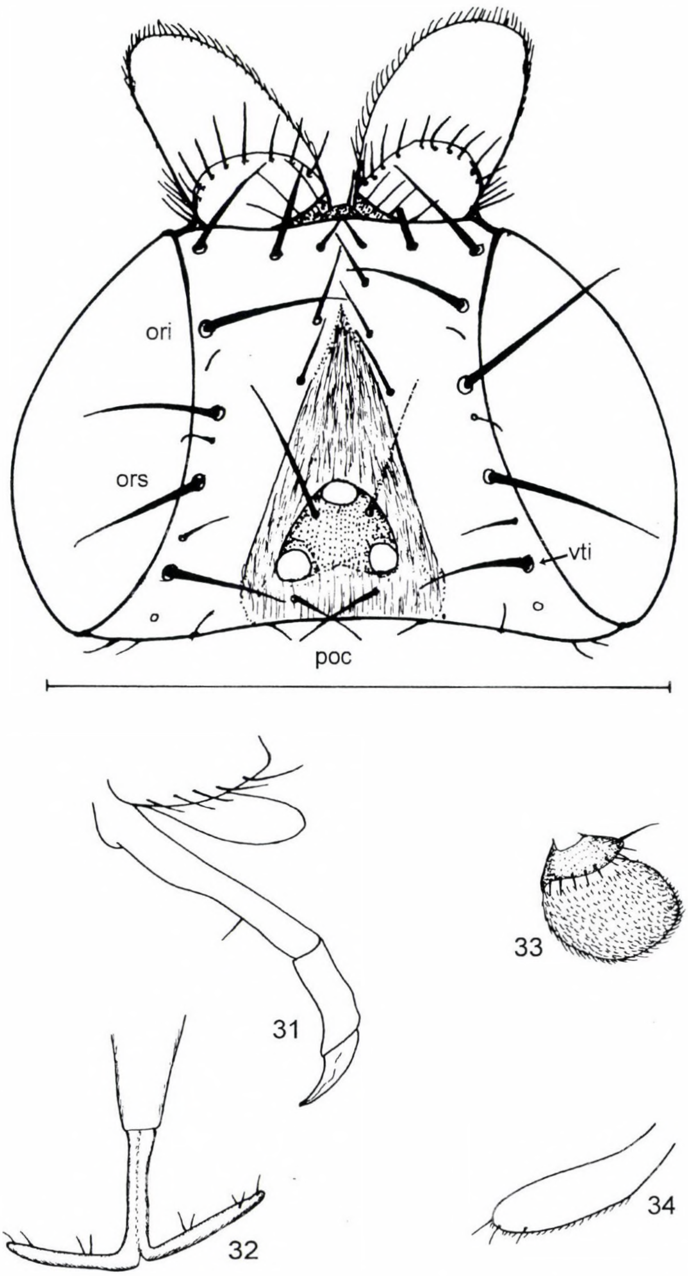
25 (24) Vein R_{2+3} runs very close to R_{4+5}. Male flagellomere less enlarged, much shorter than head (cf. Figs 9–10 of PAPP 1993) and narrower than long (Palaearctic, Hungary) *hungarica* L. PAPP, 1993

A female *Paramyia* from India (HNHM) runs here but left undescribed since there are no females of *hungarica* known (and no males from India).

26 (21) Ventral setae on hind basitarsus and second tarsomere long, i.e. longer than diameter of second tarsomere. Hind second tarsomere longer than half-length of basitarsus. In cases of bias, labium is definitely shorter than head.

27 (28) Male first flagellomere large, trapezoid-shaped (Fig. 14), i.e. upper apex protruding with a rounded dorsal apex (Philippines) **flagellomera** sp. n.

28 (27) Male first flagellomere more quadrate, upper apex less protruding and more widely rounded (3 spp., Indonesia).



Figs 31–35. *Paramyioides perlucida* sp. n., holotype male. 31 = ventral part of head with proboscis and palpus, lateral view, 32 = proboscis (labella), cranial view, 33 = antenna, medial view, 34 = palpus, medial (inner) view, 35 = head, frontal view. Scale: 0.5 mm for all

29 (30) Male surstylus in comparison to epandrium small and quadrate (Fig. 28) (Indonesia) **swanni** sp. n.

30 (29) Male surstylus rather large and rounded (Figs 25, 27).

31(32) Male distiphallus very large (Fig. 26). Male S5 broad, its setae somewhat more numerous but less long (Fig. 21) (Indonesia) **nitida** sp. n.

32 (31) Male distiphallus smaller (Fig. 24). Male S5 narrower with less but longer setae (Fig. 22) (Indonesia) **palpalis** sp. n.

Paramyioides gen. n.

Type species: *P. perlucida* sp. n. (orig. des.)
Gender: feminine.

Head. Two pairs of medioclinate *ori* setae. 3 right + 2 left, asymmetrically placed, comparatively long interfrontals (Fig. 35), plus a pair of long thin setae most cranially, laterally to *ifr*. Two pairs of very long lateroclinate *ors*, anterior pair also slightly proclinate; *oc* and *poc* pairs strong; *vti* very long, *vte* broken off from our specimen, but judging on their bases, they are probably medium-long. A pair of thin, short (0.025 mm) medioclinate, additional fronto-orbital seta between posterior *ors* and *vti*. A medium-long cervical pair present.

Frontal triangle bright yellow, reaches to 2/3 of frons (Fig. 35), frons mat yellow, ocellar triangle grey, small. Gena broad (Fig. 31). First flagellomere large, arista reduced to nil (Fig. 33). Pedicel with a medium-long dorsal seta and a wreath of short black setulae apically; scape small with ca. 4 pairs of medial, dorsomedial subapical setulae. Mouth opening extremely broad (large), but clypeus thin and half as broad. Palpi large but with 3 small thin setae on apex only (Fig. 34).

Thorax brightly shiny, translucent, i.e. its chitinous sclerites are transparent, even thoracic muscles are visible. Basisternum thin, long, triangular (this is an important synapomorphy for *Neophyllomyza* and *Paramyia*, as BRAKE (2000) has already proven it). Characteristic thoracic setae long as a whole, compared to *Paramyia* species, not the slightest sign of a second dorsocentral pair of setae. Mid and hind coxae with strong setae ventrally.

Abdomen semitransparent. Distiphallus membranous, and though not particularly long, sock-shaped similarly to the males of the *Paramyia* species. I do not want to dissect our unique specimen but partly as a consequence of its semitransparent abdomen, some characteristics of the genitalia are also detectable, as described in the description of the species.

As it is obvious from the description, most of the characteristics of *Paramyiodes* are shared with the *Paramyia* species. However, its habitus, the general impression we have got when we are looking at it, are very different. The translucent thorax and semitransparent abdomen, the large and almost bare palpus and large antenna without arista make it conspicuous. The yellow-bodied species described above are not closely related to it. I do not think that any of the recent *Paramyia* species could be, instead their stem-species is its closer relative. If so,

ranking it as a genus or subgenus, is a question of taste, better saying, weighting of the importance of the individual characteristics. Indeed, I do not want to defend its generic rank now: discovery of other species will corroborate it, or will provide facts for a ranking as a subgenus.

Paramyioides perlucida sp. n.
(Figs 31–34)

Holotype male (HNHM): TAIWAN: Taipei, Han-Lo-Da, 450 m, rocky forest undergrowth, Sep 21, 2000, leg. L. PAPP, No. 1.*

Measurements in mm: body length 1.93 (not precisely measurable owing to the down curved abdomen), wing length 1.72, wing breath 0.73.

Body yellow, brightly shiny, thorax and abdomen partly translucent/semitransparent. This is not a teneral specimen (the rigidity of its legs is wholly developed, etc.).

Head as broad as thorax. In profile head in the level of vibrissae is as long as in the level of ptilinum (head in most of the *Paramyia* species is shorter ventrally). No arista (Fig. 33). Vibrissa thin, peristomals very long, almost as long as vibrissa. Palpus 0.30 mm long, 0.11 mm at broadest.

Thoracic chaetotaxy: 1 *pprn* (humeral), 2 *np*, 1 *prsut*, 1 *dc*, 1 *sa*, 2 *pa*. Not the slightest indication of a second *dc* pair. No proepisternal, 1 large *kepst* pairs of setae. Apical scutellars 1.5 times longer than basal scutellars (the ratio is twofold in most of the *Paramyia* spp.).

Wings shiny yellowish, with microtrichia only. Costal and radial veins light yellow, other veins indistinct. Radial break of costal vein without any longer bristle. Vein R_{2+3} wavy bent (along two arcs: a smaller convex arc (seen from the costa), and a large concave arc, i.e. veins R_{2+3} and R_{4+5} convergent apically. Alula narrow, almost pointed. Vein M extremely weak, actually lost, except for its base, only the bases of trichia show its original position. Hind basitarsus without the brush of strong setae (those setae are thin and yellow).

Abdomen semitransparent, only pre-abdominal tergites are with a medial somewhat more greyish-brownish stripe each. Syntergosternite very short and weakly sclerotized. Male epandrium large, ventrally quadrate with sharp posteroventral apex, and with 3 long apical (subapical) setae. Surstylus anterior on epandrium (wholly separable from epandrium), longer than broad, rounded apically. Genitalia not prepared but distiphallus does not seem to be large.

Etymology. The Latin word *perlucida* means transparent/translucent.

*

Acknowledgements – I am very grateful to the late Dr CURTIS W. SABROSKY and to Dr IRINA BRAKE for their advice, and to Mr BEN BRUGGE of the Amsterdam Museum for his generous loan of the unique holotype of *Paramyia inconspicua* DE MEIJERE.

* Additional paratypes have been found during the proof reading stage as follows: 2 males and 1 female – same data as the holotype (found in unsorted material in 2002). The description of the male genitalia will be published in a forthcoming paper.

Mr JOHN SWANN (Royal Ontario Museum, Toronto, Canada) initiated this study and helped me much in the first phase by providing *Paramyia* material. Later we lost contact but I would like to express my most sincerely thanks also here. It is fair to assign the co-authorship of the probably most frequent Neotropical species to him, and I named also a species after him.

REFERENCES

BRAKE, I. (2000) Phylogenetic systematics of the Milichiidae (Diptera, Schizophora). *Ent. scand. Suppl.* **57**: 1–120.

HENDEL, F. (1913) H. Sauter's Formosa-Ausbeute. Acalyptrate Musciden (Dipt.). *Supplta Ent.* **2**: 77–112.

LOEW, H. (1869) Diptera Americae septentrionalis indigena. Centuria octava. *Berl. Ent. Ztschr.* **13**: 1–52.

MALLOCH, J. R. (1934) Acalyptrata (concluded). Pp. 393–489, figs 69–84, plate VIII. *In*: Diptera of Patagonia and South Chile, Part VI, fasc. 5, British Museum (Natural History), London.

MEIJERE, J. C. H. de (1916) Studien über südostasiatische Dipteren XI. *Tijdschr. Ent.* **59**: 184–213, plate 7.

OZEROV, A. (1992) Xenophyllomyza deserticola gen. et sp. n. (Diptera, Milichiidae) iz Turkmenistana. (Xenophyllomyza deserticola gen. et sp. n. (Diptera, Milichiidae) from Turkmenistan). *Vestn. zool.* **1992**(2): 18–20.

PAPP, L. (1993) Three new milichiid species (Diptera, Milichiidae) from Hungary. *Annls hist.-nat. Mus. natn. hung.* **85**: 133–139.

SABROSKY, C. W. (1965) Family Milichiidae (Phyllomyzidae, Carnidae). Pp. 728–733. *In* STONE, A. *et al.* (eds): A *Catalog of the Diptera of America north of Mexico*, Washington.

SABROSKY, C. W. (1973) 75 Family Milichiidae (Phyllomyzidae, including Carnidae). Pp. 75.1–75.12. *In* PAPAVERO, N. (ed.): A *Catalogue of the Diptera of the Americas south of the United States*, Sao Paulo.

SABROSKY, C. W. (1977) Family Milichiidae (Phyllomyzidae). Pp. 270–276. *In* DELFINADO, M. D. & HARDY, D. E. (eds): *A Catalog of the Diptera of the Oriental Region*, University Press of Hawaii, Honolulu, Vol. **3**.

SABROSKY, C. W. (1987) 79. Milichiidae. Pp. 903–908. *In* MCALPINE, J. F., PETERSON, B. V., SHEWELL, G. E., TESKEY, H. J., VOCKEROTH, J. R. & WOOD, D. M. (eds): *Manual of Nearctic Diptera*, Vol. **2**, Research Branch Agriculture Canada, Ottawa.

SABROSKY, C. W. (1989) 78. Family Milichiidae. Pp. 555–557. *In* EVENHUIS, N. L. (ed.): *Catalog of the Diptera of the Australasian and Oceanian Regions*, Bishop Museum Press and E.J. Brill, Honolulu, pp. 1155.

WILLISTON, S. W. (1897) Diptera Brasiliana. Part IV. *Kansas Univ. Quart.* (A) **6**: 1–12.

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A NEW GENUS AND THREE NEW SPECIES OF HYBOTIDAE WITH NEW RECORDS OF THE HUNGARIAN EMPIDOIDEA (DIPTERA)

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Twenty-two species are recorded as new for the Hungarian fauna, among them three species (*Tachypeza yinyang* sp. n., *Megagrapha europaea* sp. n., *Chvalaea sopianae* sp. n.) are new to science. The genus *Megagrapha* is reported from the Palaearctic region for the first time. A new genus of Ocydromiini, *Chvalaea* gen. n. (type species *Leptopeza rugosiventris* STROBL, 1910) is described with two species from Hungary.

Key words: *Chvalaea, Megagrapha*, Hybotidae, Microphoridae, Empididae, faunistic survey, new records, Hungary

INTRODUCTION

In the frame of the project "Large blank spots in the Diptera fauna of Hungary" we are to collect and to publish species representing dipterous families formerly not recorded from Hungary. Furthermore, species representing not recorded genera are also targets of our activity. Four years of the project (1999–2002) comprise a reasonable period of time, for which a fair support is provided for true faunistical studies. The results are included also in the "*Checklist of the Diptera of Hungary*" (PAPP *et al.* 2001). In the first two years of the project these collectings resulted in capturing specimens of numerous genera and species new for the fauna of Hungary. We published a paper with some new records on Empidoidea last year (PAPP & FÖLDVÁRI 2000), further results are reported in this paper.

All the specimens below are deposited in the Diptera collection of the Department of Zoology, Hungarian Natural History Museum, Budapest (below: HNHM).

Some abbreviations used below and also on collection labels: NP: Nemzeti Park [National Park], TK: Tájvédelmi Körzet [Landscape Protected Area], TT: Természetvédelmi Terület [Nature Reserve], hg., hegys.: hegység [mountains]. The following Hungarian words are on numerous labels: "csapda": trap, "erdő": forest, "rét": meadow, "patak fölött": over the brook, "patak fölött és mellett": over and alongside the brook; völgy, v: valley; p, patak: brook. The months are given as on the collection labels, i.e., May: május, 05., June: június, 06., July: július, 07., October: okt., 10., etc.; since labels are written in Hungarian, months come first.

HYBOTIDAE

Megagrapha europaea sp. n.
(Figs 1–5)

Holotype male: Kelet-Mecsek TK, Komló: Zobákpuszta, Hidasi-völgy – patak fölött, mellett, 2000. június 13., leg. PAPP L.

Paratypes: 1 male, 2 females: same as for holotype; 1 female: Zempléni TK: Regéc, Ördög-v., patak fölött és mellett, 2000. július 5., leg. PAPP L.; 1 male: Kelet-Mecsek TK: Óbánya, Óbányai-p. fölött és mellett, 2000. június 14., leg. PAPP L. (wings prepared on a slide, body with genitalia in a plastic microvial with glycerine, head and left fore leg glued on a small card under the microvial, right fore tibia and tarsi lost).

Measurements in mm: body length 1.54 (holotype), 1.50–1.55, 1.71–1.83 (paratype males, females), wing length 1.96 (holotype), 1.83–1.95, 2.05–2.25 (paratypes), wing breadth ca. 0.75 (holotype), 0.82, 0.79–0.96 (paratypes, not measurable on one of the males).

Male head and abdomen black, thorax yellow but pronotal region with proepisternal depression, and metanotum, scutellum with a prescutellar mesonotal area, also black. Female body all black.

Head actually without characteristic setae: ocellars hairlike, vertex and occiput with a number of thin white hairs. Eyes meet in the facial area, eyes densely and comparatively long pubescent. Frons (praefrons) shiny, very narrow anteriorly. Scape small, pedicel somewhat larger, first flagellomere ca. 1.5 times longer than broad (0.086 mm vs 0.055 mm), i.e. not as in *M. platytarsis*, see fig. 4 of CHILLCOTT and TESKEY (1983). Arista (Fig. 2) 0.26 mm long, somewhat thickened with dense, long cilia.

Thorax without characteristic setae, or rather, they are not longer and thicker than the enlarged microchaetae. In any case, 1 longer prescutellar dorsocentral pair and a row of 4 pairs of notopleurals (all pale yellow) are discernible. Scutellum with 4 pairs of marginal *sc*, which emerge on small tubercles.

Legs clear yellow, incl. tarsi. Legs without armature, male mid tarsi normal (Fig. 3), mid basitarsus 1.5 times longer than second tarsomere (the latter not broadened).

Wings clear with long microtrichia (Fig. 1), veins yellow. Costal cilia up to 0.085 mm. Subcostal vein weak, discontinued at about its distal 3/5 towards costa. Vein R_1 short, costal sections 2:3:4 = 85:69:30. Vein R_{4+5} slightly upcurved in its basal part, but apically downcurved, consequently, 4th costal section much shorter than 1/2 length of the 2nd section. R-M and dM-Cu cross-veins meet, their length ratio is 3 to 5 (R-M and their meeting point discoloured). Distal section of the cubital vein 0.60 mm, i.e. considerably longer than proximal section. Anal vein thin but discernible and continued along a wide arc, rather close to the wing margin, well distally to the dM-Cu cross-vein. Alula small with long bristles. Knob of halteres black, stalk yellowish.

Abdominal terga and sterna weakly sclerotized.

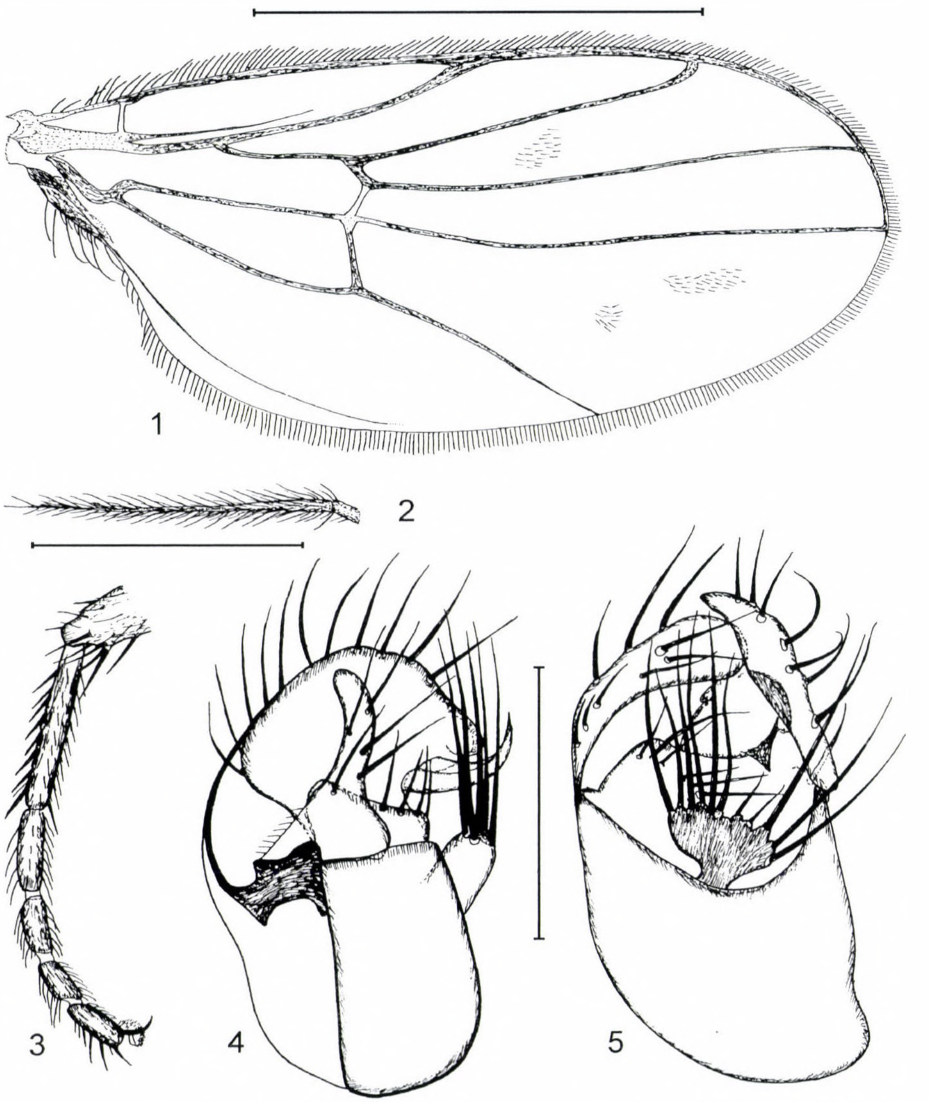
Male genitalia with fused and asymmetrical cerci, with asymmetrically placed long apical setae (Figs 4–5). Right lamella narrow, digitiform in profile, left lamella very large, continued ventrally, with a narrow recurving process subbasally (Fig. 4).

Female cerci medium-long with short hairs only.

Similar to *M. platytarsis* CHILLCOTT, 1983 but smaller (wing length 1.83 to 2.25 mm, vs. 2.4–2.6 mm that of *M. platytarsis*), its male mid second tarsomere is much shorter than first one (basitarsus), and knob of halteres is dark, not yellow as

in *M. platytarsis*. The male first flagellomere is strongly and also costal ratios are slightly different from those of *M. platytarsis*.

Etymology. This is the first known species of the genus *Megagrapha* Melander, 1928 from Europe (and also from the Palaearctic region).



Figs 1–5. *Megagrapha europaea* sp. n., paratype male. 1: wing; 2: arista; 3: male mid leg, anterior view; 4: genitalia, dorsolateral view; 5: genitalia, dorsal view. Scales: 1.0 mm for Fig. 1; 0.2 mm for Fig. 2; 0.3 mm for Figs 4–5

Tachypeza yinyang sp. n.
(Figs 6–10)

Holotype male: K-Mecsek TK: Óbánya, Óbányai-völgy, patak fölött, 1999. május 30., leg. PAPP LÁSZLÓ.

Paratypes: 1 male (abdomen with genitalia in a plastic microvial with glycerine): Melegmányi-völgy TT: Pécs, Nagy-mély-v., patak fölött, 1999. május 27., leg. PAPP LÁSZLÓ; 1 male (teneral but intact specimen): Kőszegi TK: Kőszeg, Hármas-p. fölött és mellett, 2000. június 28., leg. PAPP L.

Measurements in mm: body length 3.33 (holotype), 2.50, 3.30 (paratypes), wing length 3.58 (holotype), 3.21, 3.70 (paratypes), wing breadth 1.18 (holotype), 1.00, 1.17 (paratypes).

Body grey microtrichose but pleura darker with distinct reflection.

Head higher than long, occiput convex, antennae inserted slightly dorsally to middle of head seen in profile. Antennae yellow, arista microtrichose, 0.80 mm long. Occiput with 2 pairs of thick short setae: 0.10 mm and 0.075 mm long; plus a wreath of medium-long whitish setae around the neck and posteriorly on gena (like in *T. truncorum*). Palpi with pale terminal bristles.

Only 1 (posterior) pair of notopleurals and a pair of strong, widely separated scutellars; both pairs are very thick. Acrostichal and dorsocentral microchaetae are scarce and almost indiscernible. No dorsocentrals, in the place of posterior *dc*-s a pair of thin short hairs (only 0.02 mm long!). Scutellars (paratype) 0.16 mm long.

Legs mostly yellow, mid and hind coxae blackish, apical tarsomeres darkened; tibial and femoral structures and armature are similar to those of *T. truncorum*. Fore coxae without black spines, yellow, anterior apical 3/5 with a black stripe, which widens apically. Fore tibia robust (Fig. 6), both laterally and medially (posteriorly and anteriorly) with a black band: anteriorly in apical half, posteriorly in apical 3/5. Anterior surface of fore femora (Fig. 6) medially with sharply margined black pattern, which resembles to the Chinese yin and yang; fore femur without long dark hairs subapically (as in *T. truncorum*). Mid femur (Fig. 7) black in proximal third, dilated basally with a slight emargination subbasally, this basal part with 5 or 6 spine-like setae ventrally. Mid tibia with a larger emargination subapically (Fig. 7). Hind femur thin, black basally, which turns to dirty yellow apically. Hind tibia black in its apical fifth.

Wings light greyish with distinct brown hue along R_1, R_{4+5} and Cu veins and also by anal vein stump (CuA_2); brown colour widens into an obscure spot at fork of R_{2-5}. Vein M strongly upcurving, conjointment with costa is before wing apex. Costa and apical half of vein R_1 merge into a blackish brown flat structure.

Male cerci (Fig. 9) strongly asymmetrical: right cercus simple, left cercus with a rather sharp apical projection medially and with another process ventro-laterally. Also the bristles are asymmetrically placed on cerci. Right paramere (Fig. 8) very large in three lobes, medial one with stronger setae. Left lamella (Fig. 10) rather large but more simple, laterally-subapically with a short but sharp incision.

Female unknown.

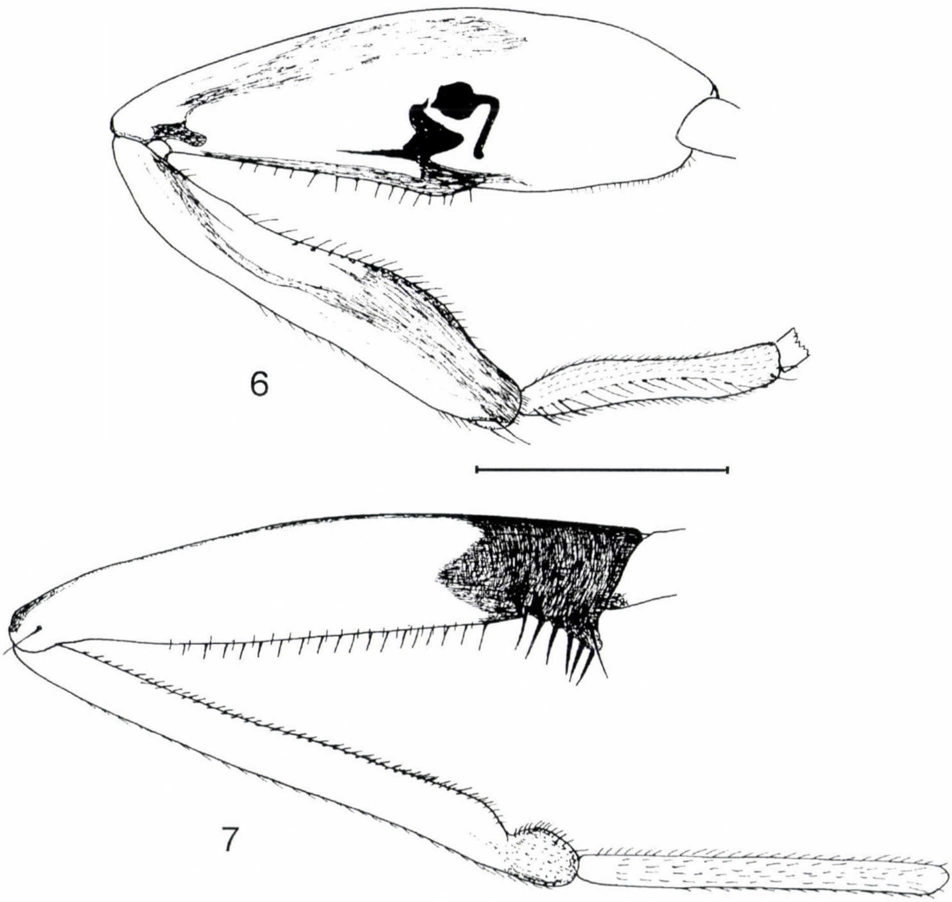
Tachypeza yinyang sp. n. is a very easily recognisable species. Actually it does not fit into the key of CHVÁLA (1975): its thoracic pleura are with a distinct reflection (like those of *T. fuscipennis*) but its scutellar setae are widely separated. It has only one pair of (posterior) notopleurals and no dorsocentrals. The black pat-

tern on the anterior surface of fore femur and tibia, the structure and colour of mid femur and tibia, as well as the single pair of notopleurals and the lack of dorsocentral setae make it conspicuous. Its male genitalia are also distinctive.

Tachypeza fennica TUOMIKOSKI, 1932 – 1 male: Bakonyszentlászló, Vinye, Cuha-szurdok, 2000. július 26., leg. PAPP [L.], BAJZA [Zs.]. New to Hungary.

Tachydromia carpathica CHVÁLA, 1966 – 1 male, 1 female: Kelet-Mecsek TK, Komló: Zobákpuszta, Hidasi-völgy, patak fölött és mellett, 2000. július 13., leg. PAPP L. 1 male: Zempléni TK: Regéc, Ördög-völgyi patak fölött és mellett, 2000. július 3., leg. PAPP L. New to Hungary.

Tachydromia woodi (COLLIN, 1926) – 1 male: Lasztonya [Zala megye], 1967. VI. 27., leg. MÓCZÁR L. New to Hungary.



Figs 6–7. *Tachypeza yinyang* sp. n., paratype male. 6: fore femur and tibia, anterior view; 7: mid femur and tibia, anterior view. Scale: 0.5 mm

Dysaletria nigripennis CHVÁLA, 1975 – 1 male, 1 female: Budapest, Pestszentlőrinc, Péterhalmi-erdő, erdei tisztás [forest clearings], 2001. 04. 29–30., leg. PAPP L. The genus and species are new for the Hungarian fauna. This species was described from Slovakia (Plešany, Král'ovský Chlmec) not far from the northern border of Hungary.

Trichina pallipes (ZETTERSTEDT, 1838) – 2 males, 1 female: Duna-Ipoly NP: Szokolya, Szén-p. fölött és mellett, 2000. május 13., leg. PAPP L. First record from Hungary.

Trichinomyia flavipes (MEIGEN, 1830) – 1 female: Aranyosgadány, hullott körtéről [fallen pear], 1970. VII. 30., leg. PAPP L.; 1 female: Újhuta, Zoltán-forr. [spring], 1960. V. 8., leg. Z SEBESS; 2 females (without heads): Kőkapu, forrás és forrásláp [spring and peat-bog], 1960. V. 7., leg. Z.SEBESS. WÉBER (1983) published it from the Barcs Juniper Woodland Nature Reserve, but we did not find the voucher specimen (male) in any of the materials we had got from the Pécs University. Consequently, one may regard the above data as the first reliable record from Hungary.

Oedalea apicalis LOEW, 1859 – 1 female: Duna-Ipoly NP: Szokolya, Szén-p. fölött és mellett, 2000. május 13., leg. PAPP L. First record from Hungary.

Oedalea hybotina (FALLÉN, 1816) – 1 female: Gagyvendégi, akácos széle [edge of a black-locust (*Robinia*) forest], 2000. 05. 16., leg. PAPP L. First record from Hungary.

Chvalaea gen. n.
(Figs 11–16)

Type species: *Leptopeza rugosiventris* STROBL, 1910
Gender: feminine.

Eyes bare and not meeting above antennae (dichoptic), but meet along their whole length below eyes (no postfrons, "face"), dorsal ommatidia of the same size as ventral ones in females. Frons (praefrons) small and rather narrow. Eyes large, gena very narrow, occiput convex (but not strongly), covered by numerous medium-long setulae. No characteristic setae on head. First flagellomere more or less long and narrow with pin-like arista (Figs 13–14). Proboscis very short.

Mesonotum extremely convex (bulging), pronotum comparatively very large (Fig. 11), which make their habitus peculiar: if abdomen placed horizontally, head is ventral to thorax*. Scutellum is reduced to a small, blunt transverse process dorsally to a large metanotum. Laterotergite bare.

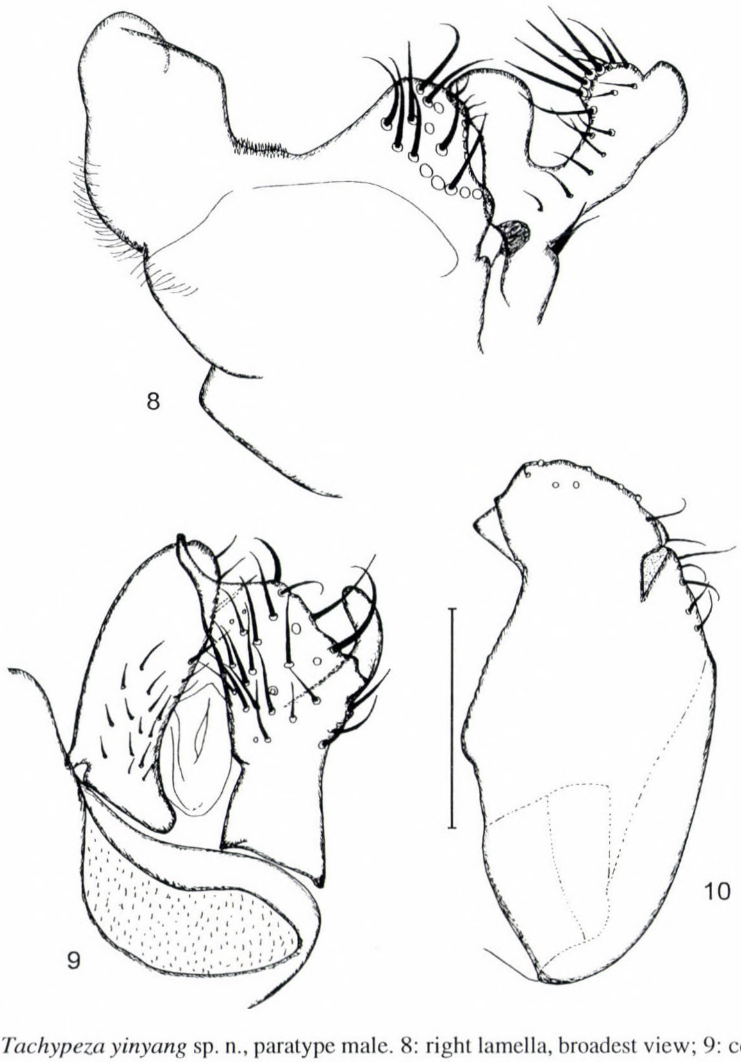
Legs with long slender setae, which are two or even three times as long as the femoral or tibial diameter at their emergence. Fore coxa short (without peculiar setae), fore, mid and hind coxae not far from each other. Legs are not raptorial as for the structure of femora and tibia, but tarsi tend to incurve with strong 5th segment and claws. Femora and tibiae long, slender. Swelling of the fore tibial gland well-discernible on medial basal surface.

Wings clear, long and comparatively narrow. Wings without axillary angle, anal lobe or alula (Figs 11–12). Costa without erect setae, nor other veins setose. Subcosta incomplete, not reaching costa. Rs originating much distally to level of cross-vein H, R-M at about middle of wing. Vein R_{4+5} terminates at apex of wing. Basal radial and basal medial cells are very long, basal medial cell termi-

* According to our friend, Dr BÉLA DARVAS (pers. comm.) *Chvalaea* specimens must fly with their abdomen lowered in order to have their ocelli dorsal, which is vital for perception of any movement over the animal, i.e. for its survival. If this is true, their legs are most anteral when flying.

nates well distal to R-M. Cell *dm* very long and distally placed. Two veins emitted from cell *dm* (M_1 lost), which do not reach wing margin. Vein CuA2 oblique and S-shape curved, posterior cubital cell only half as long as basal medial cell. Anal vein long, wavely curved, ends free somewhat distal to the middle of wing.

Abdomen long, straight (stiff), subcylindrical, abdominal sclerites heavily sclerotized, punctate. Female cerci short and hidden in the 8th segment. Since male is unknown, after the capture of a male it will be necessary to supplement this description with the features of the male genitalia.



Figs 8–10. *Tachypeza yinyang* sp. n., paratype male. 8: right lamella, broadest view; 9: cerci, broadest view; 10: left lamella, broadest view. Scale: 0.2 mm

This is one of the genera, which were mentioned as "undescribed genus B" in SINCLAIR and CUMMING (2000). We do not think this new genus would be closely related to *Oropezella* COLLIN; only the long cell *dm* and shape of the basal part of wing are shared characters.

Etymology. We name this new genus after Dr MILAN CHVÁLA (Charles University, Prague) for his unparalleled achievements in the taxonomy of the family Hybotidae and other families of Empidoidea.

Chvalaea rugosiventris (STROBL, 1910)
(Figs 14, 16)

Material studied: 1 female: Melegmányi[-völgy] TT: Pécs, Melegmányi-völgy, patak fötött és mellett, 2000. június 15., leg. PAPP.

Body length (measured in the thorax-abdomen axis) 4.30 mm, wing length 4.00 mm, wing breadth 1.14 mm.

Body colours as in *Ch. sopianae*. Body ratios even more extreme than in *Ch. sopianae*, since the abdomen 3.32 mm long, thorax 0.98 mm long.

Head 0.59 mm long. First flagellomere only slightly longer than scape and pedicel combined; antenna 0.405 mm long, arista curved (i.e. not precisely measurable, but longer than 0.55 mm, i.e. actually probably somewhat longer than 0.60 mm (Fig. 14).

Pronotum 0.17 mm, metanotum 0.31 mm if measured dorsally. Legs long, slender, e.g. hind femur 1.54 mm, with long slender bristle: longest bristle on hind tibia 0.22 mm, diameter of tibia there 0.12 mm, longest bristle on mid tibia 0.28 mm, diameter of tibia there 0.09 mm. Fore coxa dark, short, 0.35 mm, hind coxae yellow, middle coxae intermediate (but as short as hind ones). Hind femur with a badly defined dark subapical ring, hind tibia dark in its apical 3/5 part. Tarsi wholly spirally incurved with strong claws, tarsomeres darker. Wings clear, long and comparatively narrow (length/width ratio 3.5!). Wing otherwise similar to that of *Ch. sopianae*.

Abdomen extremely long, straight, abdominal sclerites heavily sclerotized, punctate. Longest (submarginal) abdominal hairs 0.40 mm long. Female 8th segment cylindrical (Fig. 16), 0.56 mm long, so longer than that of *Ch. sopianae*, but its dorsal caudal swelling indistinct (caudal edge rather upcurved).

First record for Hungary.

Chvalaea sopianae sp. n.
(Figs 11–13, 15)

Holotype female: Melegmányi[-völgy] TT: Pécs, Melegmányi-völgy, patak fölött és mellett, 2000. június 15., leg. PAPP. Paratypes: 2 females: same as for holotype.

Measurements in mm: body length (from the most anterior point of thorax to the end of abdomen) 4.38 (holotype), 4.38, 4.47 (paratypes), wing length 4.28, 4.26, 4.32, wing breadth 1.28, 1.28, 1.34.

Body peculiar: head ventral to the thorax-abdomen axis (Fig. 11), thorax dark brownish grey, slightly dusted, postpronotal callus and postalar callus diffuse reddish, abdomen shiny black, rugose (punctate). Body ratios somewhat less extreme than in *Ch. rugosiventris*, since the abdomen 3.32–3.36 mm long, thorax in the abdominal axis 1.10 mm long. Legs mostly yellow but knees dark.

Head 0.51–0.59 mm long. Eyes dichoptic and bare, but meet along their whole length below eyes, dorsal ommatidia of the same size as ventral ones. Frons (praefrons) small and as narrow at ocelli as diamater of fore knee. Gena very narrow, occiput convex, covered by a number of light, medium-long setulae. No characteristic setae on head. Palpi extremely short, only 0.07 mm, also proboscis very short, 0.10 mm. Scape and pedicel only slightly longer than half length of first flagellomere, the whole antenna slightly shorter than arista (Fig. 13): antenna of the holotype 0.517 mm, arista 0.56

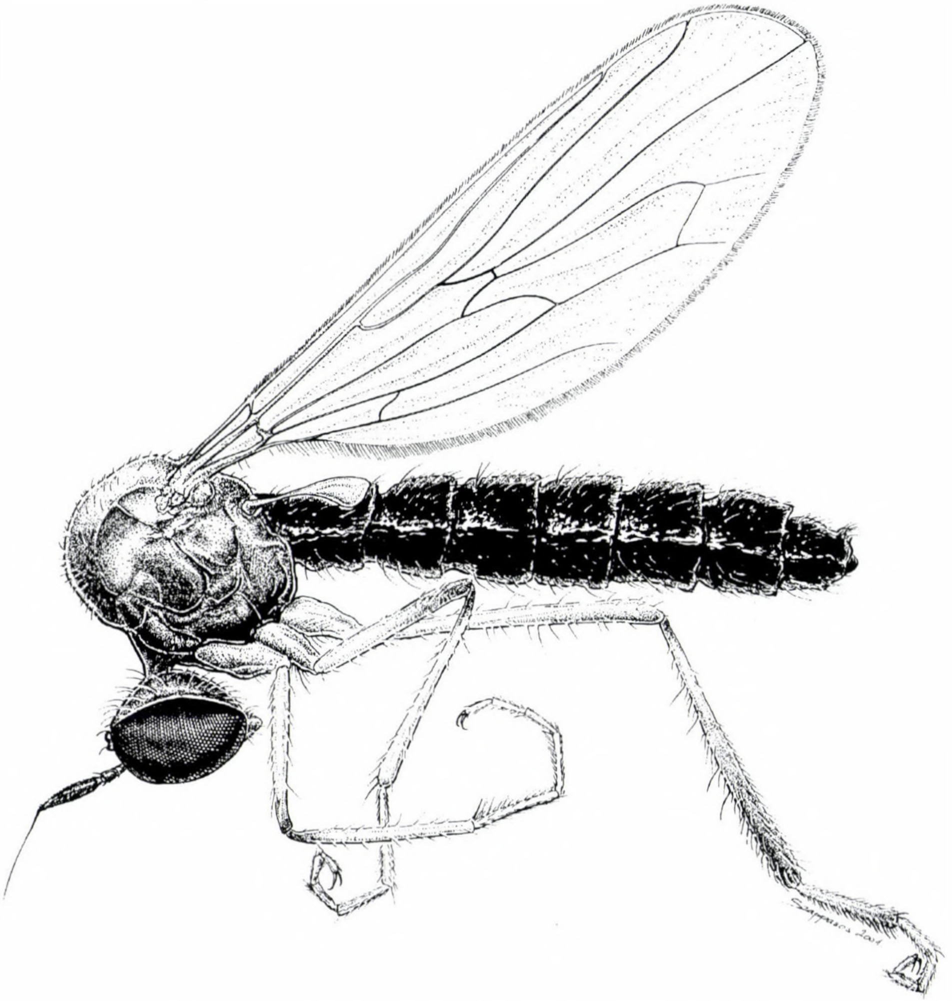
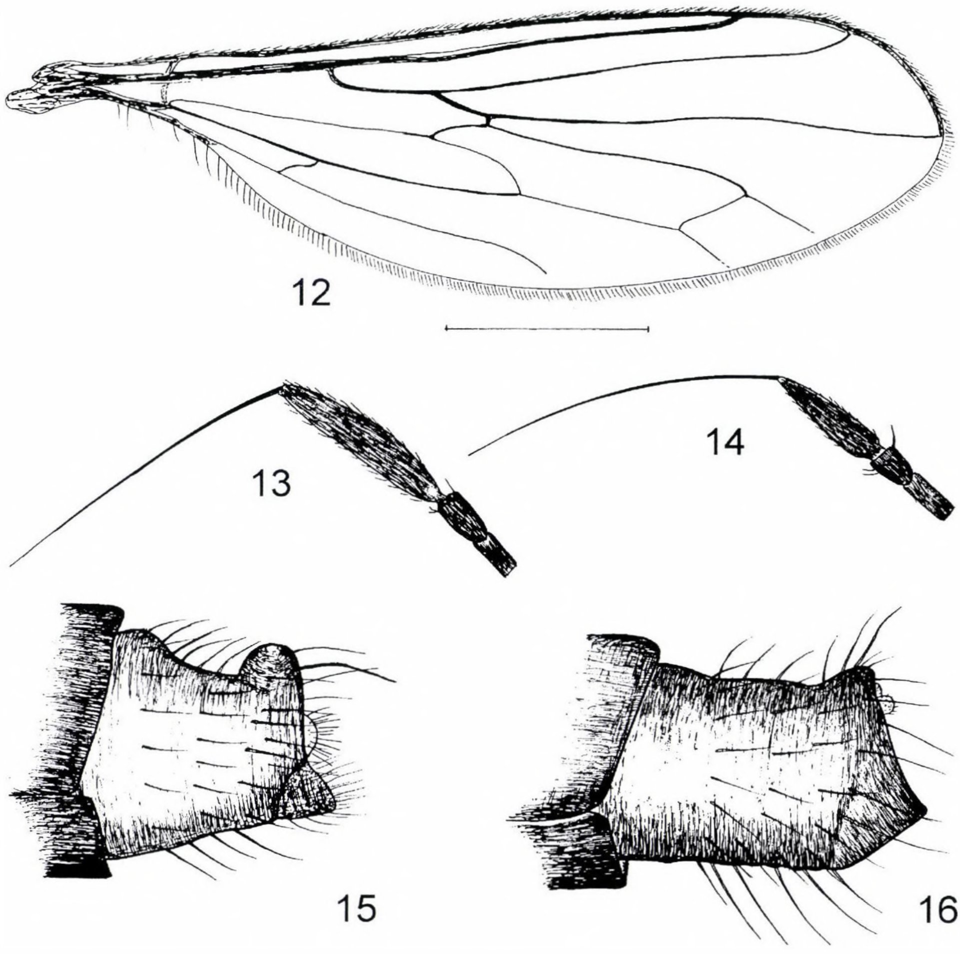


Fig. 11. *Chvalaea sopianae* sp. n., paratype female, habitus

mm, ratio 1.08 (one of the paratypes: 0.53 mm, 0.57 mm, broken off on the other one). First flagellomere definitely longer than that of *Ch. rugosiventris*.

Mesonotum extremely convex (bulging), pronotum 0.18 mm, metanotum 0.33 mm if measured dorsally. Scutellum minute, laterotergite bare. Thoracic setae much reduced: only 1 weaker postpronotal (humeral), which is 0.10 mm on one paratype; 1 pair of stronger posterior notopleurals (0.22 mm long on one paratype), no more characteristic setae on thorax.

Legs long, slender, e.g. hind femur 1.54 mm, with long slender bristle: longest bristle on hind tibia 0.26 mm, diameter of tibia there 0.12 mm, longest bristle on mid tibia 0.26 mm. Fore coxa dark, short, 0.38–0.40 mm, hind coxae yellow, middle coxae intermediate (but as short as hind ones).



Figs 12–16. 12: *Chvalaea sopianae* sp. n., female wing. 13–14: female antenna, medial view: 13: *Ch. sopianae* sp. n.; 14: *Ch. rugosiventris* (STROBL). 15–16: female 8th abdominal segment, lateral view: 15: *Ch. sopianae* sp. n.; 16: *Ch. rugosiventris* (STROBL). Scales: 1.0 mm for Fig. 12, 0.5 mm for Figs 13–16

Swelling of the fore tibial gland rather large, tibia at widest 2 times as broad as subapically. Hind femur with a badly defined dark subapical ring, hind tibia mostly dark, at most basally lighter. Tarsi wholly spirally incurved with strong claws, yellowish, hind tarsomeres darker.

Wings clear (Fig. 12), long and comparatively narrow (length/width ratio 3.27–3.47). Wing otherwise similar to that of *Ch. rugosiventris*. Halteres waxy yellow, 0.71–0.77 mm long, distal part of stalk very thin.

Abdomen extremely long, straight, abdominal sclerites heavily sclerotized, punctate. Longest (submarginal) abdominal hairs 0.36 mm long. Eighth abdominal segment much shorter than that of *Ch. rugosiventris*: female 8th segment (Fig. 15), 0.91 mm long measured at middle height, dorsocaudally with a large globular swelling (Fig. 15) (caudal edge 0.64 mm high). Last visible sternite (most likely the 9th) with dense white hairs (Fig. 15). Female cerci must be short, hidden in the 8th segment.

All the three individuals are slightly damaged: wings of the holotype are splitted; left wing of one of the paratypes was much wrinkled, now glued on a card below the specimen in a less wrinkled position; antennae of the other paratype are lost, right wing of this specimen is mounted on a slide.

Based on STROBL's (1910) description of *Leptopeza rugosiventris*, SINCLAIR and CUMMING (2000) were able to point out that the species must belong to an undescribed genus. However, the description itself: "Die Legeröhre bildet eine dicke, ebenfalls grobpunktierte Röhre von der Länge der halben Breite des letzten Ringes..." and "Die Fühler sind etwas länger als das 3. Fühlerglied", was not enough to make distinction between the two species as *L. rugosiventris* was captured together with the females of another species. In any case, to adduce full proof, it was necessary to study the type of *L. rugosiventris*. Dr MILAN CHVÁLA was kind enough to study the type of *L. rugosiventris* in STROBL's Collection for us (pers. comm.). The new species *Ch. sopianae* is easily distinguishable from *Ch. rugosiventris* by its antennae and by the shape of its 8th abdominal segment.

Etymology. The specific epithet "sopianae" (noun) is the old Roman name of the city Pécs, where this new species originates from.

MICROPHORIDAE

Microphor crassipes MACQUART, 1827 – 2 males: [Duna-Ipoly NP] Diósjenő, Kemence-patak, 1995. VI. 20., leg. PAPP L., Ádám L. A species new for the Hungarian fauna (this is the third known species in our country).

EMPIDIDAE

Hilara albiventris VON ROSER, 1840 – 1 male: Zempléni TK: Nagyhuta, Kemence-patak égeresei [forest with *Alnus*], 2000. júl. 6., leg. PAPP L. A species new for the Hungarian fauna.

Rhamphomyia (Pararhamphomyia) tipularia (FALLÉN, 1816) – 1 male: Duna-Ipoly NP: Szokolya, Szén-p. fölött és mellett, 2000. május 13., leg. PAPP L. CHVÁLA and WAGNER (1989) listed it also from Hungary, but we do not know voucher specimen(s) from the modern Hungary. WÉBER (1975) did not include it in his Fauna Hungariae part, not even as a species expected to occur.

Chelifera flavella (ZETTERSTEDT, 1838) – 1 male: Zempléni TK: Regéc, Ördög-völgyi patak fölött és mellett, 2000. július 3., leg. PAPP L. WÉBER's (1975) specimens (1 male, 3 females: Kőszegi-hg., Velemi-erdő, 1960. VII. 11., leg. Mihályi/Zsirkó) were revised and we found that they belong to *Ch. trapezina*. Consequently this is the first reliable record for this species from Hungary.

Dolichocephala engeli NIESIOLOWSKI, 1992 (*Dolichocephala engeli*: VAILLANT, 1978) – 6 males (leg. L. PAPP): Zempléni TK: Regéc, Ördög-völgy, patak fölött és mellett, 2000. 07. 03.; 1 male: K-Mecsek TK: Komló, Zobákpuszta, Hidasi-völgy, patak fölött, 1999. május 26.; 1 male: Kőszegi TK: Kőszeg, Hármas-p. fölött, mellett, 2000. június 28.; 1 male: A[ggteleki] NP: Szin, Patkós-völgy, 400 m, patakpart, 1988. IX. 12–13.; 2 males: B[ükki] NP: Miskolc, Garadna-völgy, patakpart, 1990. IX. 27. First records for Hungary.

Dolichocephala guttata (HALIDAY, 1833) – 9 males (leg. L. PAPP): 1 male: Pécs, Éger-völgy, patak fölött, mellett, 2000. 06. 16.; 1 male: K-Mecsek TK: Komló, Zobákpuszta, Hidasi-völgy, Petasitetum, 1999. május 28.; 4 males: K-Mecsek TK: Óbánya, Óbányai-völgy, patak fölött, 1999. május 25.; 1 male: ibid., patak fölött, mellett, 2000. június 14.; 1 male: [Duna-Ipoly NP] Szendehely, Keskeny-bükki-p. völgye, patakpart [beside the brook], 1997. V. 21.; 1 male: Gerecse TK: Tata-Agostyán, Bocsájtó-völgy [valley], tisztás [clearing], 1990. IX. 7. (plus 10 females of the *D. guttata*-group in the HNHM). First records for Hungary.

Dolichocephala ocellata (COSTA, 1954) – Mecsek Mts, leg. L. PAPP: 1 male: K-Mecsek TK: Komló, Zobákpuszta, Hidasi-völgy, patak fölött, 1999. május 26.; 1 male: ibid., Petasitetum, május 28.; 2 males, 4 females: Melegmányi TT: Pécs, Nagy-mély-v., patak fölött, 1999. május 27.; 1 male: ibid., patak fölött, mellett, 2000. június 15.; 1 male, 1 female: ibid., Melegmányi-völgy, patak fölött, mellett, 2000. június 15.; 1 male, 2 females: K-Mecsek TK: Óbánya, Óbányai-völgy, patak fölött, 1999. május 25/26. First records from Hungary.

Dolichocephala thomasi WAGNER, 1984 – 1 male: Zempléni TK [Regéc], Ördög-völgy, Malaise-csapda, 1999. június 8., leg. PAPP L., Szappanos A. This is the first record of this species from Hungary.

Clinocera (Kowarzia) barbatula (MIK, 1880) – 1 male: Kőszegi TK: Kőszeg, Hétvezér-forrás [spring], patak fölött, 2000. 07. 25., leg. PAPP L. Another species new for the Hungarian fauna; its closest relative, *C. (K.) tenella* WAHLBERG, 1844 was published as new to Hungary last year (PAPP & FÖLDVÁRI 2000).

Wiedemannia sp. – 1 female: Kács, vízimalom zúgója [at a water-mill], 1955. VIII. 18., leg. Z. Sebess. Its head and most of the legs are lost. This is obviously a *Wiedemannia* species but it cannot be identified in its damaged state and because of its sex. Otherwise it would be the first reliable record of the *Wiedemannia* as genus from Hungary. WÉBER (1975) keyed 18 species of this genus from Hungary. However, all but one of their names were published in square brackets (i.e. as species expected to occur). The occurrence of "*Eucelidia Zetterstedti* Wlk." at Budapest, which was published by THALHAMMER (1900) and quoted by Wéber, is improbable, as we (PAPP & FÖLDVÁRI 2000) noted last year.

*

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REFERENCES

CHILLCOTT, J. G. & TESKEY, H. J. (1983) A revision of the New World genera allied to Megagrapha Melander (Diptera: Empididae). *Canad. Ent.* **115**: 1291–1328.

CHVÁLA, M. (1975) The Tachydromiinae (Dipt. Empididae) of Fennoscandia and Denmark. *Fauna ent. scand.* **3**: 1–336.

CHVÁLA, M. (1983) The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna ent. scand.* **12**: 1–279.

CHVÁLA, M. & WAGNER, R. (1989) Family Empididae. Pp. 228–336. *In* SOÓS, Á. & PAPP, L. (eds) *Catalogue of Palaearctic Diptera, vol. 6.* Akadémiai Kiadó, Budapest.

COLLIN, J. E. (1961) Empididae. Pp. 1–782. *In British Flies*, vol. 6. Cambridge Univ. Press, Cambridge.

PAPP, L. & FÖLDVÁRI, M. (2000) Empidoidea (Diptera): genera and species new to Hungary. *Folia ent. hung.* **61**: 239–244.

SINCLAIR, B. J. & CUMMING, J. M. (2000) Revision of the genus Apterodromia (Diptera: Empidoidea), with a redefinition of the tribe Ocydromiini. *Records of the Australian Museum* **52**: 161–186.

STROBL, G. (1910) Die Dipteren von Steiermark. II. Nachtrag. *Mitt. naturw. Ver. Steierm.* **46**(1909): 45–293.

THALHAMMER, J. (1900) Diptera, pp. 1–76. *In A Magyar Birodalom Állatvilága, Fauna Regni Hungariae* vol. 3. A K. M. Természettudományi Társulat, Budapest. [in Latin and Hungarian]

WAGNER, R. (1984) Aquatische Empididen (Diptera) aus hessischen Mittelgebirgen und angrenzenden Gebieten. *Beitr. Naturkde Dresden* **19**(1983): 135–146.

WÉBER, M. (1975) 28. család: Táncoslegyek–Empididae. *Magyarország Állatvilága (Fauna Hungariae)* **14**(13): 1–220. Akadémiai Kiadó, Budapest. [in Hungarian]

WÉBER, M. (1976) Magyarország Empididae (Diptera) fajainak faunakatalógusa. *Pécsi Tanárk. Főisk. Tud. Közlem., Ser. 7, Biol.* **20**: 3–33. [in Hungarian with German summary]

WÉBER, M. (1983) Újabb adatok a barcsi borókás Empididae (Diptera) faunájáról [Recent data on the Empididae fauna (Diptera) of the Juniper woodland of Barcs, Hungary]. *Dunántúli Dolg. Term. Tud. Sor. Pécs* **3**: 76–81.

WÉBER, M. (1987) The empidid fauna of the Kiskunság National Park (Diptera), pp. 251–257. *In* MAHUNKA, S. (ed.) *The Fauna of the Kiskunság National Park, vol. 2.* Akadémiai Kiadó, Budapest.

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A NEW SPECIES OF FILATIMA BUSCK, 1939 (LEPIDOPTERA, GELECHIIDAE) FROM TRANSYLVANIA, ROMANIA

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A new species of Gelechiidae, the *Filatima transsilvanella* sp. n., closely allied to the Asian *F. autocrossa* (MEYRICK, 1937) is described from steppe habitats of Transylvania (Romania). With 16 figures.

Key words: Palaearctic, *Filatima transsilvanella*, Gelechiidae, new species, Romania

INTRODUCTION

The genus *Filatima* BUSCK, 1939, comprises about 100 described species, the majority in the Nearctic region, a small number in the Neotropical region and about 20 species in the Palaearctic region. During very successful collecting activity in the steppe-like hilly habitats of the Transylvanian Basin we found a *Filatima* species, which we could not identify with the help of the recently published comprehensive works on the European gelechiid moths (ELSNER *et al.* 1999, HUEMER & KARSHOLT 1999). After studying further publications on the Palaearctic *Filatima* (ANIKIN & PISKUNOV 1996, BIDZILYA *et al.* 1998, CARADJA & MEYRICK 1937, CLARKE 1969, IVINSKIS & PISKUNOV 1981, 1989, PISKUNOV 1981) and after consultation with specialists on Palaearctic and Nearctic Gelechiidae it emerged that we had found a previously undescribed species.

Filatima transsilvanella sp. n.

Holotype: Câmpia Transilvaniei, Viişoara (Câmpia Turzii), 4. IV. 1998 (♂), legit S. KOVÁCS & Z. KOVÁCS, coll. Hungarian Natural History Museum, Budapest, Hungary (HNHM).

Paratypes: 140 ♂♂, 30 ♀♀: same data as holotype (12 ♂♂); same locality as holotype, 15. V. 1993 (3 ♂♂); 1. VI. 1996 (4 ♂♂, 4 ♀♀), (gen. prep. no. 911 (♂) KOVÁCS and 920 (♀) KOVÁCS); 17. V. 1997 (5 ♂♂), (gen. prep. no. 912(♂) KOVÁCS); 23. IV. 1998 (6 ♂♂); 04. 05. 2000 (35 ♂♂), (gen. prep. no. 1338(♂) KOVÁCS); 27. 05. 2000 (62 ♂♂, 26 ♀♀), (gen. prep. no. 1413(♀) KOVÁCS and 1433(♀) KOVÁCS); 30. 04. 2001 (12 ♂♂), leg. & coll. S. KOVÁCS & Z. KOVÁCS, Sf. Gheorghe, Romania; 2 ♂♂, 1 ♀ in coll. Natural History Museum, London, Great Britain; 2 ♂♂, 1 ♀ in coll. Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria; 2 ♂♂, 1 ♀ in coll. US National Museum of Natural History, Washington, D.C., U.S.A.; 2 ♂♂, 1 ♀ in coll. "Grigore Antipa", National Museum of Natural History, Bucharest, Romania; 1 ♂, 1 ♀ in coll. HNHM; 1 ♂, 1 ♀ in coll. Zoologisk Museum,

University of Copenhagen, Copenhagen, Denmark; Munții Apuseni, Cheile Turzii, 16. V. 1993. (♂), (gen. prep. no. 5001(♂)) O. KARSHOLT, legit S. KOVÁCS & Z. KOVÁCS, coll. Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark.

Description of the male (Fig. 11): Wingspan 20 mm. Labial palpus light brown, segment 2 with moderately broad scale brush beneath, slightly lighter on lower surface. Face and head light brown. Antenna dark brown. Thorax and tegula brown. Forewing slender; brown, mottled with orange; a slightly elongate black spot in fold, two further spots in cell, proximal rounded, distal elongated and curved, all three surrounded by orange; subapical spot indistinct, orange; row of small black dots on termen; basal half of fringes pale orange mottled with brown, distal half grey beyond black fringe line. Underside of forewing uniform brown, with yellowish sheen. Hindwing rather broad, termen weekly emarginate beneath apex, grey, fringes yellowish grey. Underside of hindwing grey with yellowish sheen, with "curtain fringe" of long narrow scales along radius and further fringe between veins CuA2 and CuP (Fig. 14). Abdominal tergites I–III pale orange, IV–VIII brown, with dense cover of distinct orange scales arising from inner surface of sternite VIII. Abdominal sternites brown. Legs brown.

Variation: The wingspan of the males in the type-series varies from 17 to 20 mm. Dependent on the variable degree of orange mottling the forewings may appear brownish orange (Fig. 12) to brown (Fig. 13). In lighter specimens dark brown patches are visible at the base of the forewing, in the middle of the fold and also between the distal spot in the cell and the tornus. Along the termen there is a dark brown broken line rather than a row of small black dots. In dark specimens all abdominal tergites are brown and the orange bunches of scales on segment VIII are less distinct.

Female (Figs 15, 16): Wingspan 17–18 mm. Similar to male, labial palpus variable, light brown to orange mottled with brown; both pairs of wings narrower and more pointed; black spots sometimes large, orange lining almost absent; orange transverse fascia at three-quarters narrow or separated into costal and tornal spots; orange scales on abdominal segment VIII absent. Underside of hindwing without "curtain fringes".

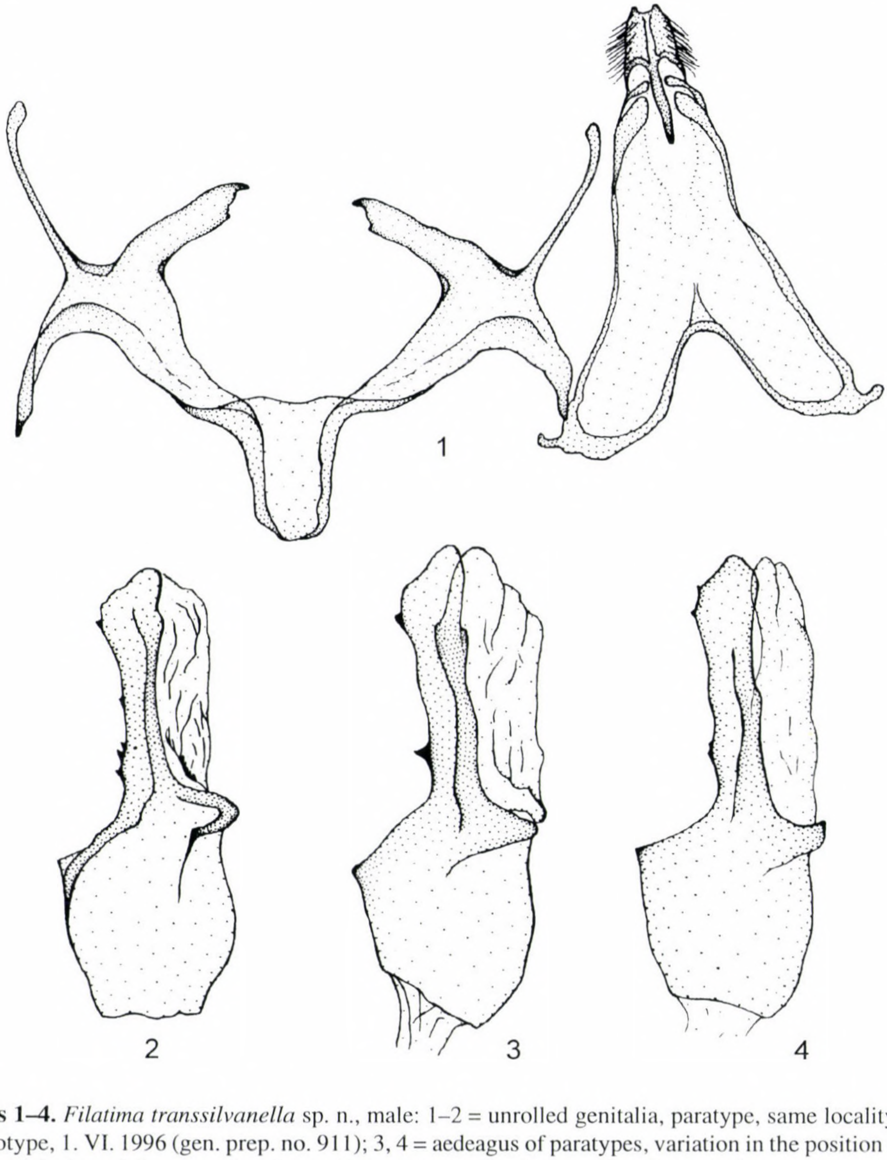
Male genitalia (Figs 1, 2): Uncus narrow, gradually broadened anteriorly; gnathos hook stout, short; tegumen evenly broadened from uncus to pedunculi, deeply emarginate anteriorly; valva slender, straight, distally curved and slightly broadened; sacculus at right angles to valva, straight, with small claw on apex, about two-thirds length of valva, relatively broad, but more then three times longer then wide; vinculum long and slender; saccus deep, U-shaped; anellus weakly sclerotized, without pair of lobes; aedeagus very broad, with long ribbon-like sclerotization set with minute lateral thorns, vesica without cornuti.

Variation. In some paratypes (Figs 3, 4) slight variation is observed in the position and size of the lateral thorns on the ribbon-like sclerotization of the aedeagus.

Female genitalia (Figs 5–7): Papilla analis oval, weakly sclerotized; apophyses posteriores very long, rod-like; segment VIII simple, weakly sclerotized; apophyses anteriores slightly longer than segment VIII, rod-like; ostium bursae with pair of large, rounded, distinct, ear-like lateral sclerites; antrum strongly sclerotized; ductus bursae short, with weak longitudinal folds and long, irregular, ribbon-like asymmetrical sclerotization extended over corpus bursae; sub-oval corpus bursae moderately large, distally covered with spines; signum small rounded plate, with pair of long, acute teeth; by the junction of ductus and corpus bursae membranous accessory bursa with rolled tubular structure.

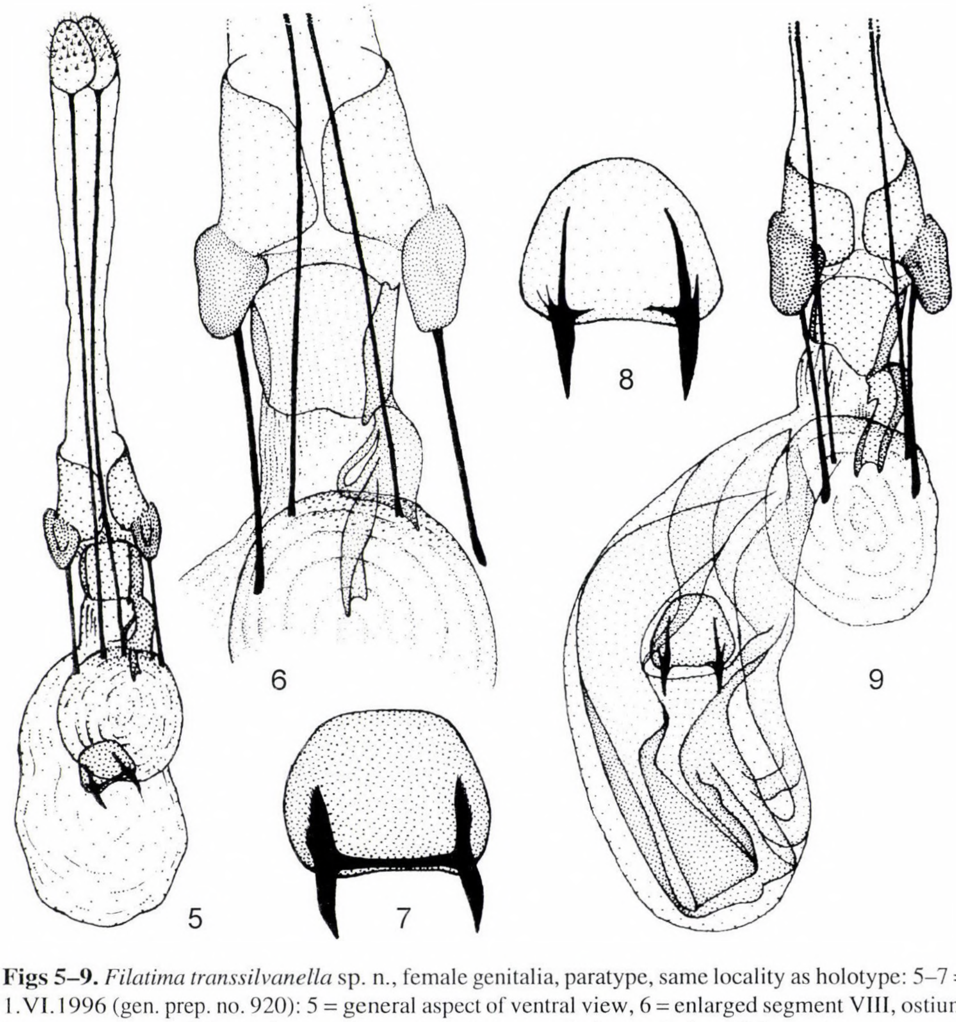
Variation (Figs 8, 9): Only slight variation is observed in the form of strongly sclerotized irregular, ribbon-like asymmetrical sclerotization of the distal part of ductus bursae and in the form of signum. By one specimen corpus bursae filled with extended, moderately sclerotized, irregular ribbon-like sclerotization.

Taxonomic notes: The intrageneric relationships between the about twenty known Palaearctic *Filatima* species are far from clear. Light specimens of *Filatima transsilvanella* sp. n. resemble in their wing pattern *F. zagulajevi* ANIKIN et PISKU-



Figs 1–4. *Filatima transsilvanella* sp. n., male: 1–2 = unrolled genitalia, paratype, same locality as holotype, 1. VI. 1996 (gen. prep. no. 911); 3, 4 = aedeagus of paratypes, variation in the position and size of the lateral thorns on the ribbon-like sclerotization: 3 = same locality as holotype, 17. V. 1997 (gen. prep. no. 912), 4 = same locality as holotype, 4. V. 2000 (gen. prep. no. 1338)

NOV, 1996, although the former is probably not closely allied to any of its European congeners. The structure of the male genitalia is similar to that of the eastern Palaearctic *Filatima autocrossa* (MEYRICK, 1937) but is distinguished in the aedeagus which in the latter bears a strong serrated median spine at right angles to the longitudinal axis (CLARKE 1969: 91, fig. 3a). Both species share a very interesting character, the presence of both radial and cubital "curtain fringes" of long



Figs 5–9. *Filatima transsilvanella* sp. n., female genitalia, paratype, same locality as holotype: 5–7 = 1.VI.1996 (gen. prep. no. 920): 5 = general aspect of ventral view, 6 = enlarged segment VIII, ostium bursae, antrum and ductus bursae, 7 = enlarged signum; 8–9 = variation of ductus bursae, corpus bursae and signum, 17.V.1997 (gen. prep. no. 1413): 8 = general aspect of ventral view (excepting papillae anales), 9 = enlarged signum

posteriorly-directed scales on the underside of the hindwing. This is seen as an indication of a close relationship between *Filatima autocrossa* (MEYRICK, 1937) and *F. transsilvanella* sp. n. None of the European possesses a "curtain fringe", with the exception of *F. spurcella* (DUPONCHEL, 1843), in which only a radial fringe is present (SATTLER, pers. comm.). The male genitalia also resemble those of an as yet undescribed Iranian species which, however, lacks "curtain fringes" (HUEMER, pers. comm.). The structure of the female genitalia is similar to that of *Filatima spurcella* (DUPONCHEL, 1843).

Distribution: Only known from the type locality and neighbouring areas (Fig. 10).

Biology: Host-plant and early stages unknown. Adults have been collected from early April to early June in a steppe habitat at light and are fairly common in the type locality. Females emerge much later than males.

Habitat: The new species was discovered on west- to south-west-exposed slopes in the western, most arid, hilly part of the Transylvanian Basin. These slopes

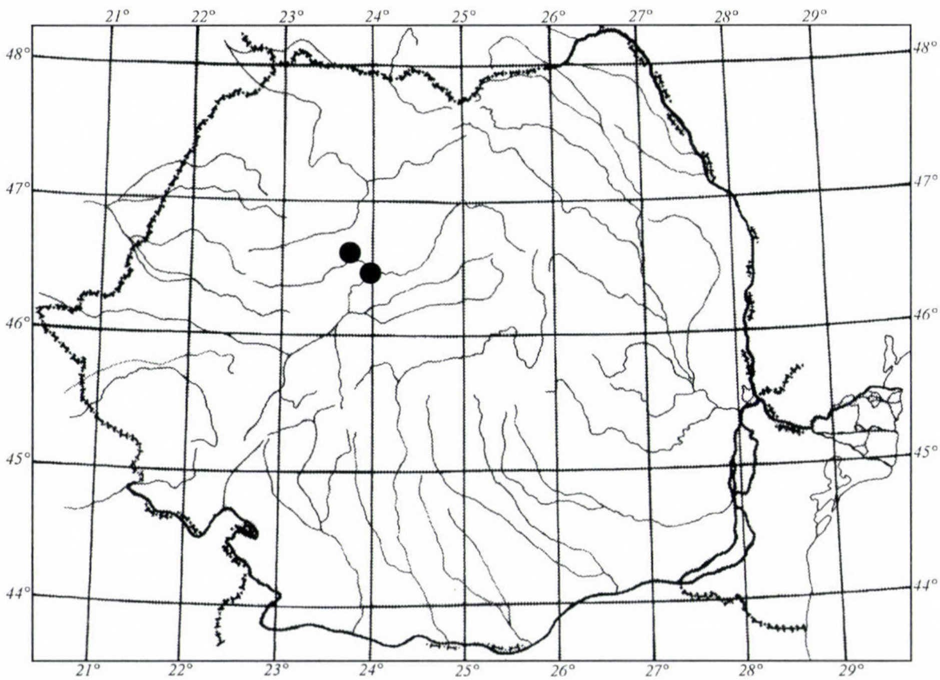
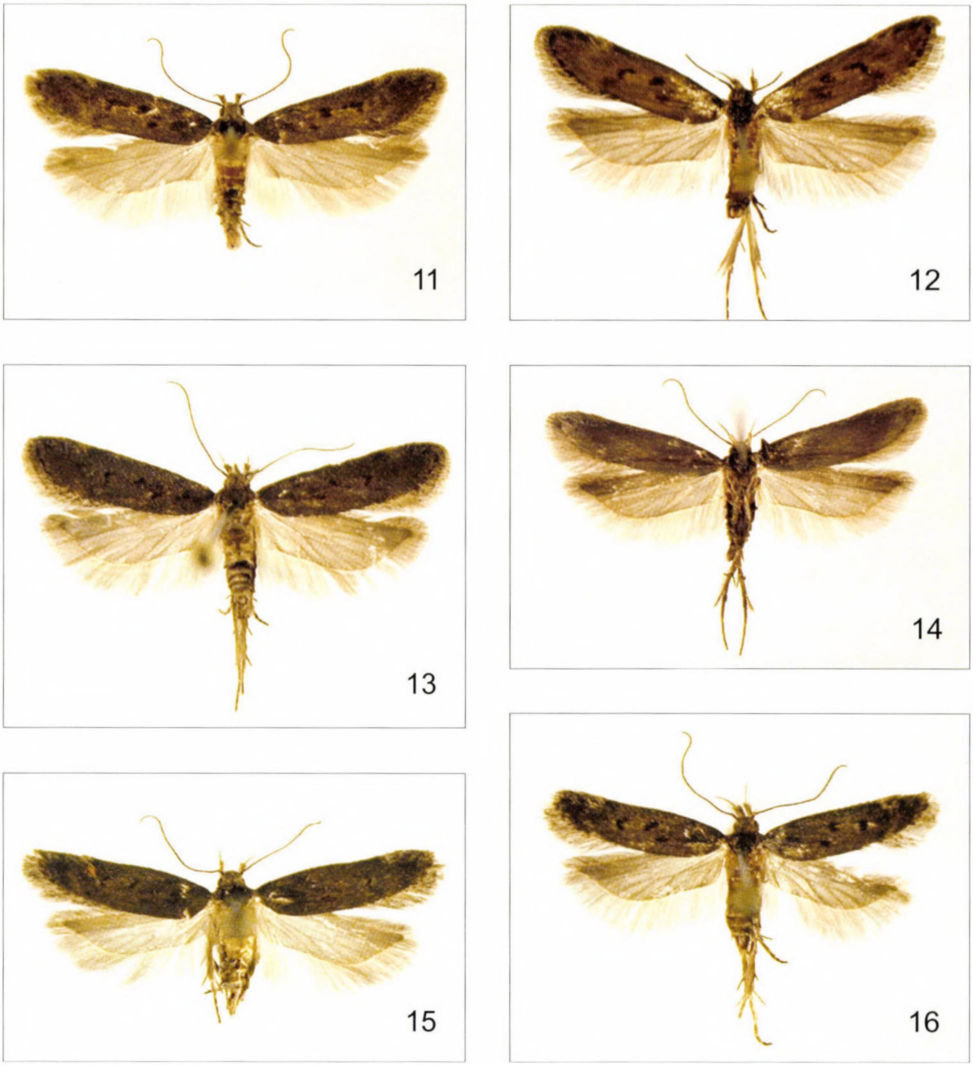


Fig. 10. Distribution map of *Filatima transylvanella* sp. n. in Romania



Figs 11–16. *Filatima transsilvanella* sp. n.: 11 = holotype, 12 = male, paratype, light coloured specimen: same data as holotype, 13 = male, paratype, dark coloured specimen: same locality as holotype, 4.V.2000, 14 = male, paratype – underside of hindwing with the "curtain fringes": same data as holotype, 15 = female, paratype, same locality as holotype, 27.V.2000, 16 = female, paratype, specimen with large black spots: same locality as holotype, 27.V.2000 (12–16 deposited in coll. S. KOVÁCS & Z. KOVÁCS, Sf. Gheorghe, Romania)

are covered with authentic steppe vegetation rich in eastern floral elements. A number of very interesting additional faunistic records were obtained in the same locality: *Scrobipalpa (Euscrobipalpa) brahmiella* (HEYDEN, 1865), *Syncopacma incognitana* GOZMÁNY, 1957, (KOVÁCS & KOVÁCS 2000), *Cochylimorpha fucatana* (SNELLEN, 1883), *C. subwoliniana* (DANILEVSKIJ, 1962) (first European record), *Aethes caucasica* (AMSEL, 1959), *Muschampia cribrellum* (EVERSMANN, 1841), *Pseudophilotes bavius hungaricus* (DIÓSZEGHY, 1913), *Scotopteryx ignorata* HUEMER et HAUSMANN, 1998, *Autophila dilucida* (HÜBNER, 1808), *Cucullia mixta* FREYER, 1841, *Oncocnemis confusa* (FREYER, 1842), *Mesotrosta signalis* (TREITSCHKE, 1829), etc. The second locality, where a single male specimen was found, is a lime-stone gorge in the immediate neighbourhood of the hilly Transylvanian Basin, where steppe vegetation can be found as well.

Etymology: The name alludes to the Latin name of Transylvania where the species was detected.

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REFERENCES

ANIKIN, B. V. & PISKUNOV, V. I. (1996) New species of gelechiid moths from Saratov Province, Russia (Lepidoptera: Gelechiidae). *Zoosyst. Rossica* **4**: 171–175.

BIDZILYA, O. V., BUDASHKIN, YU. I. & KOSTYUK, I. YU. (1998) Additions to the fauna of Microlepidoptera of Transbaikalia. *J. Ukr. ent. Soc.* **4**(1–2): 33–63. [In Russian]

CARADJA, A. & MEYRICK, E. (1937) Materialien zu einer Lepidopterenfauna des Taishanmassivs, Provinz Shantung. *Dt. ent. Z. Iris* **50**: 157.

CLARKE, G. (1969) Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. **7**: 90–91, pl. 45.

ELSNER, G., HUEMER, P. & TOKÁR, Z. (1999) *Die Palpenmotten (Lepidoptera, Gelechiidae) Mitteleuropas. Bestimmung – Verbreitung – Flugstandort – Lebensweise der Raupen.* Bratislava. 208 pp.

HUEMER, P. & KARSHOLT, O. (1999) Gelechiidae I (Gelechiinae: Teleiodini, Gelechiini). *In* HUEMER, P., KARSHOLT, O. & LYNEBORG, L. (eds): Microlepidoptera of Europe 3. Apollo Books, Stenstrup, 356 pp.

IVINSKIS, P. & PISKUNOV, V. I. (1981) Revue of Palearctic species of genus Filatima Busck, 1939 and description of new female of species Filatima ukrainica Piskunov, 1971, femina nova (Lepidoptera, Gelechiidae) found on Lithuanian coast of the Baltic Sea. *Lietuvos TSR Mokslu Akademijos darbai. C serija* **4**: 47–52. [In Russian]

IVINSKIS, P. & PISKUNOV, V. I. (1989) Two new species of the genus Filatima (Lepidoptera, Gelechiidae) from Central Asia. *Nasekomye Mongolii* **10**: 572–577. [In Russian]

KOVÁCS, Z. & KOVÁCS, S. (2000) The commented checklist of Gelechiidae (Lepidoptera) of Romania. *Entomol. Rom.* **4**: 11–44.

PISKUNOV, V. I. (1981) Gelechiidae. Pp. 659–784. *In*: MEDVEDEV, G., S. (ed.): *Opredelitelj nasekomykh Evropejskoj Ciasti SSSR. IV Cheshuekrylyle 2.* Nauka, Leningrad. [In Russian]

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NEW NOCTUIDAE TAXA FROM TAIWAN AND THE ADJACENT REGIONS (LEPIDOPTERA), II.

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Descriptions of three new Noctuidae genera, *Egiropolia* gen. n., *Orthopolia* gen. n. and *Taeneremina* gen. n. and seven new species, *Anorthoa changi, Egiropolia kingmana, Orthopolia scotoptera, O. gonggashana, Dryobotodes caerulescens, Potnyctycia nemesi* and *Taeneremina scripta* spp. n. from Taiwan are given. With 35 figures.

Key words: Noctuidae, new genera, new species, China, Taiwan, Vietnam

INTRODUCTION

The systematic re-arrangement of the Noctuidae collection of the Taiwan Forestry Research Institute, Taipei and the National Museum of Natural Science, Taichung and the treatment of new expedition materials of Taiwanese and Hungarian lepidopterists resulted in the discovery of numerous new Noctuidae taxa and several, as yet unsolved, taxonomic and nomenclatural problems have been recognised. The second item of the series dealing with the taxonomic novelties of the research on the Noctuidae fauna of Taiwan contains the descriptions of a part of the new genera and species which were found during the above-mentioned studies.

Abbreviations: TFRI – Taiwan Forestry Research Institute, Taipei; HNHM – Hungarian Natural History Museum, Budapest; NMNS – National Museum of Natural Science, Taichung.

SYSTEMATIC PART

Anorthoa changi sp. n.
(Figs 1, 2, 17, 18)

Holotype: female, "TAIWAN, Prov. Taitung, Yu-shan National Park, Tatachia, 2610 m, 16.II.1999, leg. L. Peregovits & G. Ronkay"; slide No. RL6641 (coll. G. RONKAY, in HNHM Budapest). Paratypes. Taiwan, 1 male, Prov. Taichung, Anmashan, 2100 m, 14.II.1997, leg. H.R. Tzuoo; 2 males, 3 females, from the same site, 10.II.1998, leg. C. M. FU (coll. C. M. FU, Taiping and H. R. TZUOO, Puli).

Slide Nos RL7076 (male).

Diagnosis: The new species represents the only known relative of the eastern Nepalese *Anorthoa rubrocinerea* (HREBLAY et RONKAY, 1998), forming a rather remote species group within the genus (see RONKAY *et al.* 2001). The colouration of the two species is conspicuously different (see Figs 1, 2, and HREBLAY & RONKAY 1998, Pl. 146, Figs 15, 16; HREBLAY & RONKAY 1999, Pl. 14, Fig. 6), but the presence of the characteristic glaucous zone between the postmedial and subterminal lines of the marginal area and the configuration of the genitalia of both sexes show, however, their close relationships.

Anorthoa changi differs externally from *A. rubrocinerea* by its much paler, nearly unicolorous orange-brownish forewing ground colour, the absence of the intense, dark, reticulate irroration, the less defined crosslines and median area, the paler hindwing, etc. The male genitalia of the two species are easily distinguishable by the shape of the valva, the size and shape of the harpe and the structure of the carina penis and the vesica, respectively (see Fig. 17 and HREBLAY & RONKAY 1999, Fig. 15). The apical part of the valva of *A. changi* is evenly tapering towards small, triangular, apically finely pointed cucullus, that is acutely triangular with long, wedge-shaped pollex in *A. rubrocinerea*. The harpe of the new species is much larger, discoidal, the aedeagus is longer with the carina having longer but narrower, less serrate ventral bar. The vesica of *A. changi* is longer than that of its twin species and the distal part has a long, narrow cornuti field which is absent in *A. rubrocinerea*. The female genitalia of *A. changi* (Fig. 18) differ from those of *A. rubrocinerea* (see HREBLAY & RONKAY 1998, Fig. 959) by their considerably longer, narrower ostium and ductus bursae and the broader, larger, less elongate apical curve of the considerably longer appendix bursae.

The new species may also resemble certain *Orthosia* OCHSENHEIMER, 1816 (s. l.) species, the Taiwanese species of this genus are treated and illustrated in detail by CHANG (1991), HREBLAY and RONKAY (1997, 1998), RONKAY and RONKAY (2000) and SUGI (1955, 1982, 1986). *Anorthoa changi* can easily be separated, however, from all of them as none of the eastern Pacific *Orthosia* species have similar, conspicuously pale zone in the inner half of the marginal area and silvery-white fore tibiae, and the features of the genitalia of both sexes, especially the configuration of the vesica and the appendix bursae, serve as a good base for distinguishing *A. changi* from the related taxa of *Orthosia*.

Description. Wingspan 30–34 mm, length of forewing 15–16 mm. Sexes similar. Head relatively small, palpi slender, porrect, with rather long, cuneate third segment; male antenna finely dentate, with long, loosely fasciculate cilia, that of female filiform, shortly ciliate. Pubescence of head and thorax rather homogeneous, deep ochreous brown or rufous brown, ventral side darker; fore tibiae conspicuously silvery white with fine, blackish tripe along inner margin. Forewing elongate, rather narrow, with pointed apex and more or less straight outer margin along termen. Ground colour unicolorous, dark ochreous brown or pale rufous brown, with very fine darker brown, blackish and

whitish grey irroration; costa somewhat paler. Wing pattern obsolescent, traces of antemedial and postmedial lines and median fascia usually recognisable as pale brownish-greyish shadows. Outlines of orbicular and reniform stigmata hardly traceable, sometimes slightly sharper, fine, brownish with a few whitish scales, filling of reniform usually somewhat darker brownish than ground colour, especially along inner edge and at lower third. Subterminal line fine, sinuous, silvery-whitish, inner part of marginal area between postmedial and subterminal lines widely whitish-greyish ("glaucous"). Subterminal line represented by a row of brown spots, cilia as ground colour. Hindwing shining, milky ochreous, with weak pale brownish suffusion; veins usually slightly darker, discal spot present but diffuse, transverse lines obsolescent. Terminal line interrupted, brown, cilia ochreous-whitish, with fine brownish apical spot(s). Underside of wings shining whitish-ochreous, innear area of forewing suffused with brownish, upper part of transverse line present, diffuse, discal spot hardly visible. Hindwing with weak brown irroration, being somewhat stronger along costal margin; discal spot and upper part of transverse line usually clearly recognizable.

Male genitalia (Fig. 17): Genital capsule rather small, valvae significantly shorter than aedeagus. Uncus short, flattened, lanceolate, with fine dorso-medial crest, tegumen short, narrow, penicular lobes small, weak. Fultura inferior sclerotized, short but broad, more or less subdeltoidal, transtilla heavily sclerotized, falcate, with large medio-apical field of strong teeth; vinculum strong, very long, narrowly V-shaped. Valva elongate but rather short, evenly tapering towards small, triangular, apically finely pointed cucullus. Corona weak, represented by a few setae, pollex short, more or less digitiform. Sacculus short, broad, clavus reduced, appearing as a small, setose surface. Ampulla strong, falcate, harpe flattened, discoidal-capitiform with long basal bar and with a small field of sensory setae apically. Aedeagus long, rather thick, cylindrical, arcuate; carina with long, sclerotized, eversible ventral bar, terminated in a few acute teeth and with a much shorter ventro-lateral bar on right side, having strong, triangular apical tooth. Vesica very long, tubular, membranous, helicoidal with two full coils situated rather far from each other. Basal part everted forward, broadly tubular, with small, pocket-like subbasal diverticulum; walls of basal part finely verrucose towards first, rather broad coil. Medial part narrowly tubular, recurved ventrally, second coil narrow; distal part of vesica more or less straight, narrow, its walls rather densely scobinate, armed with a long field of small, spiculiform cornuti.

Female genitalia (Fig. 18): Ovipositor medium-long, papillae anales more or less quadrangular, apophyses posteriores and anteriores slender, almost equal in length. Ostium bursae long, narrowly tubular, flattened, posterior quarter gelatinous, anterior three-quarters sclerotized, with long, narrow, densely verrucose marginal folds on dorsal side. Proximal end of ostium fused with ductus by ribbed-cristate ring; ductus bursae long, tubular, membranous-wrinkled, with long, strongly sclerotized, cristate lateral ribbon on left side, extending into basal part of appendix bursae. Appendix bursae membranous, very long, helicoid with two coils, distal end strongly dilated, apical part subconical, rugose-wrinkled. Corpus bursae ellipsoidal-ovoid, with four long but rather weak signum-stripes.

Bionomics and distribution. The new species inhabits the higher deciduous forest regions of the high mountainous areas of the Yu-Shan and the Anmashan Mts. It appears in the very early spring aspect, the few known specimens were collected at the middle of February in two subsequent years, earlier in the given years than most species of the genera *Orthosia* s. l. and *Anorthoa*.

The new species represents another typical member of Taiwanese winter fauna of Himalayan origin. *Anorthoa changi* and its twin species, *A. rubrocinerea*,

form a small species group within *Anorthoa* displaying a strongly disjunct distribution pattern. Both species are stenochorous, *A. rubrocinerea* is known from the Kanchenjunga massif in eastern Nepal, while *A. changi* is endemic to Taiwan. The transitional link(s) between the two taxa and their areas are still unknown, but supposedly occur in the higher mountainous ranges of Yuennan and northern Indochina and in the Kwangtung (Guangdong) area.

Etymology. The new species is dedicated to the late Mr. B. S. CHANG, the famous Taiwanese collector, author of several books on the Taiwanese Lepidoptera, the teacher of Mr C. M. FU and Mr H. R. TZUOO in lepidopterology.

Orthopolia gen. n.

Type species: *Polia knyvetti* HAMPSON, 1894.

Diagnosis. This another new genus of the *Egira* DUPONCHEL, 1845 generic complex (see also the diagnosis of *Egiropolia* gen. n.) contains a small group of externally very similar species of allopatric distribution. The type species, *O. knyvetti* (Figs 3, 4) is known from the southern Himalayas (Nepal, Sikkim), *O. scotoptera* sp. n. (Figs 5, 6) lives in the top region of the Fansipan Mts, N Vietnam, *O. gonggashana* sp. n. (Fig. 8) occurs in Sichuan while *O. tayal* (YOSHIMOTO, 1993) (Fig. 7) is endemic to Taiwan. These four species represent two pairs of sister species, according to the configuration of their genitalia: the *O. knyvetti–O. scotoptera* species pair is distributed in the main chain of the southern Himalayas, the *O. tayal –O. gonggashana* pair has a more northern distribution, displaying a greater disjunction between their ranges.

The species of the genus resemble mostly certain taxa of the genus *Orthosia* OCHSENHEIMER, 1816 (the *O. albiceps* (HAMPSON, 1894) species-group) and the *D.* (s. l.) *nigralba* (YOSHIMOTO, 1993) group of *Dioszeghyana* HREBLAY, 1993, but are easily distinguishable from them by the configuration of the genitalia of both sexes and also by several external features. The sister group of *Orthopolia*, according to the configuration of the genitalia of both sexes, is *Egira*, with the most closely related *Egira subterminata* (HAMPSON, 1905) species-group; their outgroup is the *Lithopolia–Kisegira–Xylopolia–Clavipalpula* lineage.

The diagnostic characteristics of the new genus are as follows: Medium-sized moths, wingspan 35–41 mm, length of forewing 16–18 mm. Head and eyes rather small, interfacetal hairs long, longer than in most related Orthosiini groups. Frons smooth, with long, rather sparse tuft; palpi elongate, narrow, with long, setiform ventral hairs, third segment fine, cylindrical. Proboscis well-developed,

long, strong. Male antenna filiform or finely dentate (*scotoptera*), with long or very long fasciculate cilia, that of female finer, filiform, sparsely, shortly ciliate; basal antennal tuft well-developed. Collar broad, whitish, generally paler than tegulae, with fine medial crest; tegulae rather distinct, broad, black(ish). Pro- and metathoracic tufts large; abdomen slender, relatively short, dorsally pinkish or ochreous-reddish with fine lateral ridges, ventral side much darker, usually blackish grey. Basal abdominal coremata absent, anal tuft weak, dorsal crest represented by a large dark tuft on second segment. Tibiae of all legs unspined, blackish, with fine white rings and short pinkish fringes. Forewing elongate, narrow, with apex pointed; outer margin finely crenulate, tornal angle rounded. Hindwing rather small, more or less rounded; its venation is rather quadrifine with vein m2 originating rather far from median fold at crossvein, stalking with it only at middle of marginal area.

Male genitalia (Figs 20–23). Uncus short, slender but strong, apically more or less hooked; tegumen weak, narrow and short, penicular lobes relatively small, narrow; lateral sclerite conspicuously long. Anal tube with sclerotized ventral side, covered with minute denticles. Fultura inferior more or less trapezoidal or subdeltoidal, vinculum long, sclerotized, V-shaped. Valvae elongate, symmetrical (*tayal, gonggashana*) or slightly asymmetrical with fine, pyramidal subapical prominence on dorsal side of right cucullus (*knyvetti, scotoptera*). Saccular part broad, relatively strongly, medial third finely, apical part strongly tapering into acute apex of cucullus. Cucullus elongate-triangular with short, weak corona (*tayal, gonggashana*) or narrow, sclerotized, wedge- or horn-shaped (*knyvetti, scotoptera*). Costal margin with rounded, convex lobe; pollex absent. Basal plate of harpe straight, long, sometimes with fine postero-lateral process, apical (erect) part much shorter, digitiform, apically setose, fused partly with base of ampulla. Ampulla rather long, slender, more or less falcate. Sacculus elongate, sclerotized, clavus lobate, large (*knyvetti, scotoptera*) or flattened (*tayal, gonggashana*), dorsal edge of sacculus with sclerotized plate distally (*knyvetti, scotoptera*) or with fine triangular process (*tayal*, less prominently in *gonggashana*); ventral edge of sacculus may be terminated in small, membranous lobe bearing long hair-pencils (*knyvetti, scotoptera*). Aedeagus medium-long, cylindrical, straight, carina with stronger, more or less scaphoidal ventral plate. Vesica rather complex, a long, broad, ventrally recurved, medially helicoid, membranous tube, with long, tubular frontal (subbasal) and subterminal diverticula. Basal tube with one (*knyvetti, gonggashana*) or two (*scotoptera*) finely serrate bars or with two small brushes of fine spinules (*tayal*), frontal diverticulum with smaller or larger, rather conical or pyramidal apical cornutus, subterminal diverticulum armed with a larger bundle of long, fine, pin-like spines.

The male genital capsula of *Orthopolia* differ from those of *Egira* (s. l.) and *Lithopolia* by the complete absence of the pollex (or pollex-like lobe) and the evenly tapering distal part of the valva while most *Egira* and *Lithopolia* species have a neck-like constriction below cucullus. The whole clasping apparatus of *Orthopolia* is much stronger, more sclerotized than that of the species of *Kisegira* HREBLAY et RONKAY, 1999, the saccular part of the valva is much broader than the distal part while in *Kisegira* the distal part of the valva is only slightly tapering of even somewhat broader than the saccular part. The valvae of *Xylopolia* and *Clavipalpula* differ from those of *Orthopolia* by having well-developed, broad cucullus with long corona.

The clasping apparatuses of *Orthopolia* and *Egiropolia* are similarly strongly sclerotized, but rather dissimilar in configuration, the valvae of *Orthopolia* are strongly tapering towards apex, while those of *Egiropolia* are much broader, with more or less parallel costal and ventral margins.

The structure of the vesica of *Orthopolia* is rather complex, significantly more sophisticated than those of all known *Egiropolia, Kisegira, Lithopolia, Xylopolia* and *Clavipalpula* species and the taxa of the eastern Asian groups of *Egira* (s. l). but less complex than those of *Egira* s. str., comprising the western Palaearctic lineages (e.g. the *E. conspicillaris* and the *E. anatolica* species-groups). The basic configuration of the vesica of *Orthopolia* and *Egira* (s. str.) is rather uniform althought differ in several details as follows: the main tube of the vesica of the species of *Egira* (s. str) is longer, having two to four cornuti in the basal part of vesica sitting on shorter or longer diverticula (*Orthopolia* has only one long frontal diverticulum, terminated in a small(er) cornutus), the distal part of the vesica is recurved and helicoid (it is recurved but not helicoid in *Orthopolia*), having two diverticula, one of them is naked (this second diverticulum is absent in *Orthopolia*). In addition, the aedeagus of *Egira* (s. str.) is considerably longer, stronger than that of *Orthopolia*, with more prominent sclerotization of the carina.

The female genitalia can be characterized by the short, weak, truncated conical ovipositor; the large, sclerotized, quadrangular or trapezoidal ostium bursae, the flattened, membranous (*tayal*) or sclerotized (*knyvetti, scotoptera*) ductus bursae, forming in latter case a firmly fused, heavily sclerotized complex of ostium and ductus bursae; the well-developed, discoidal-globular or ellipsoidal cervix bursae, with short but strong, sclerotized crest at its junction to ductus bursae; the presence of a heavily sclerotized, patch-like subapical plate (*scotoptera*) or a pouch-like proximo-lateral appendage and a sclerotized proximal area oppositely, the somewhat constricted, rugose posterior quarter of the corpus bursae and the elliptical-ovoid main part of corpus with four long, inequal signum-stripes, respectively.



Figs 1–8. 1–2 = *Anorthoa changi* sp. n.: 1 = paratype, male, 2 = holotype, female; 3–4 = *Orthopolia knyvetti* HAMPSON: 3 = male, Nepal, 4 = female, Nepal; 5–6 = *O. scotoptera* sp. n.: 5 = holotype, male, 6 = paratype, female; 7 = *O. tayal* YOSHIMOTO, male, Taiwan; 8 = *O. gonggashana* sp. n., holotype male

The female genitalia display the close relationships of *Orthopolia* with the *Egira subterminata* species-group (see Figs 24–26 and HREBLAY & RONKAY 1999, Figs 47–53), the most characteristic apomorphy of *Orthopolia* is the sclerotized proximo-lateral pouch (or the homologous, more apical sclerotized plate) of the cervix bursae; another distinctive feature of the two lineages is the configuration of the ductus bursae which is homogeneous, sclerotized or wrinkled but not separated into two differently built parts as in the *Egira subterminata* species-group and the whole ostium-ductus complex is shorter than in its sister-group.

Bionomics and distribution. An expansive eastern Himalayan group, its area extending from Central Nepal (Annapurna Himal) throughout the northernmost mountain region of N Vietnam towards Taiwan to the east and along the south-eastern frontier of the Tibetan plateau to Sichuan (Gongga Shan region). The species of the genus are characteristic of the highest deciduous forest regions, occurring above 2.000 m altitude, in certain localities even up to 3.500 m a.s.l. All known taxa are univoltine, the imagines are on the wing from the end of the winter to the mid-spring (from mid-February to May), depending on the altitude of the locality and the actual climate of the year. The moths are attracted strongly to artificial light, the early stages are undescribed.

Orthopolia scotoptera sp. n.
(Figs 5, 6, 21, 25)

Holotype: male, "VIETNAM, Prov. Lao Cai, 2650 m, Fan-si-pan Mts, 7 km W Sa Pa, 103°48'E, 22°18'N, 1–2.II.1999, leg. L. Peregovits & G. Ronkay" (coll. G. RONKAY, in HNHM Budapest).

Paratypes: 29 males, 8 females, with the same data as the holotype; 3 males, 5 females, Prov. Lao Cai, Fan-si-pan Mts, 2540 m, 6 km W Cat Cat, 103°48'E, 22°17'N, 14.III.1998, leg. L. PEREGOVITS & T. Vásárhelyi (coll. HNHM and G. RONKAY).

Slide Nos RL6165, RL7389 (males), RL6671, RL7390 (females).

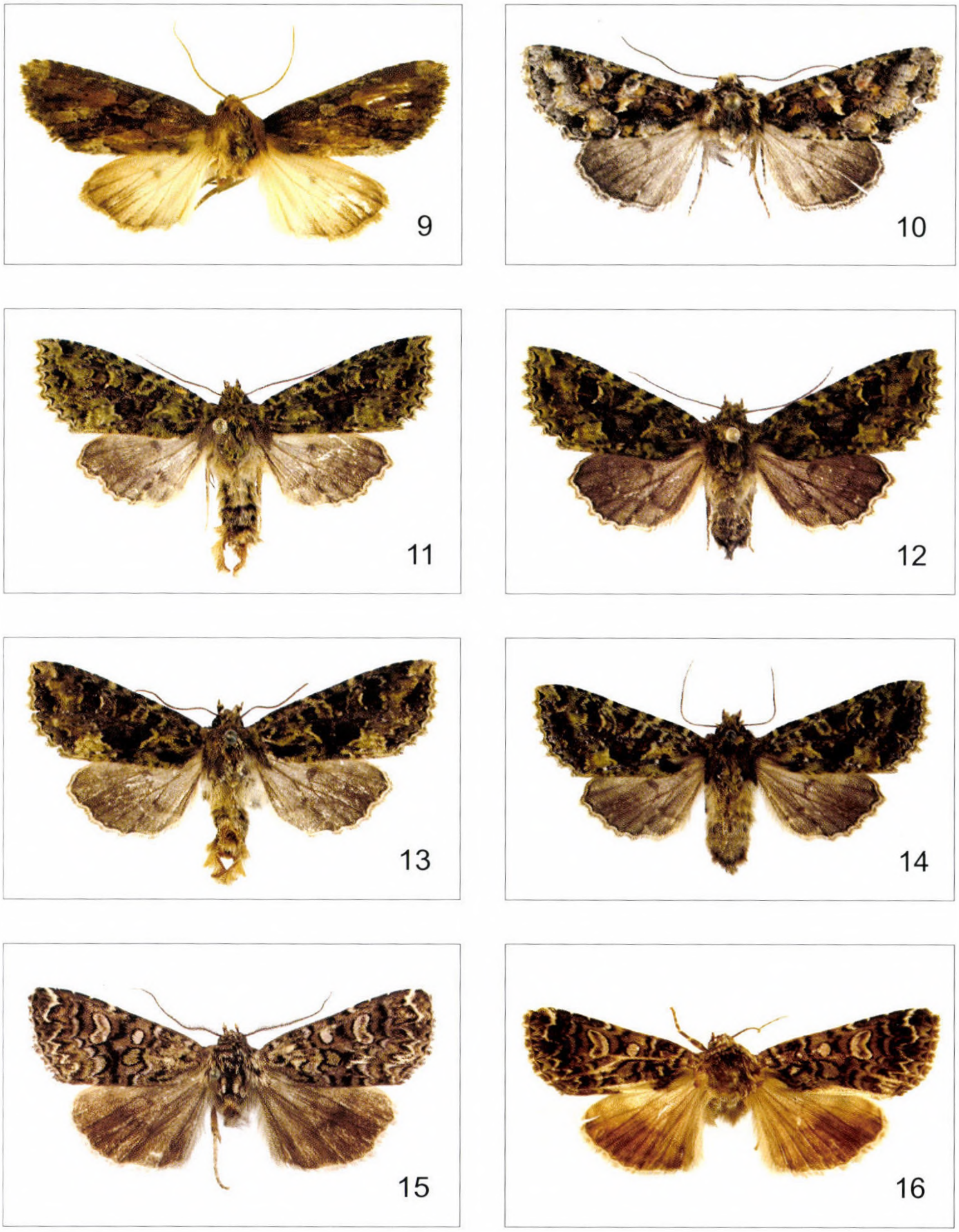
Description. Wingspan 36–40 mm, length of forewing 16–18 mm. Head and palpi blackish, tips of palpi, a stripe between antennae, parts of vertex and collar white, latter with olive-grey and a few blackish scales at upper third. Thorax broad, tegulae large, blackish mixed with claret-brown scales, base of forewing with small white tuft; pro- and metathoracic tufts small but prominent, blackish-brownish. Dorsal side of abdomen ochreous-brownish with long reddish-brown lateral ridges; dorsal crest blackish brown, consisting of large basal and tiny medial tufts; ventral side blackish grey except ochreous-reddish anal tuft. Legs blackish with white rings, tibiae with longer claret-reddish and/or pinkish fringes. Forewing elongate, narrow, with apex pointed; outer margin rather oblique, finely crenulate. Colouration of forewing rather variegate, but more unicolorous than that of its congeners; scaling finely reticulate. Ground colour dark violaceous grey, irrorated with blackish scales, outer part of basal field, subcellular zone and inner half of marginal field suffused

with rosy-grey, pinkish ochreous or pinkish-brownish scales. Basal area relatively broad, its costal area covered with white scales, basal and subbasal lines represented by black dots and lines; basal dash an acute, short black patch. Antemedial line fine, oblique, almost straight, black with whitish inner definition. Median fascia an indistinct, interrupted blackish line, postmedial line fine, simple, slightly sinuous, blackish with whitish-ochreous and pinkish outer side. Median area constricted below cell, all stigmata present, encircled fully or incompletely with fine black lines. Orbicular stigma rounded, filled with whitish, its centre rosy-grey or dark grey; reniform rather large, bean-shaped, defined with fine black and whitish annuli, filled with ground colour. Claviform stigma short, rounded, filled with dark violaceous grey; suborbicular patch most often diffuse, broad, rosy-brown or pinkish-ochreous, rarily with somewhat stronger ochreous-whitish streak at middle. Marginal area broad, inner third paler pinkish or violaceous, lightest part of wing; subterminal line fine, white, more or less continuous, angled below apex and at cubital veins, its short, reduced extensions not reaching terminal line. Inner side of subterminal defined with thre large blackish patches, outer side with smaller black dots in dark violaceous grey zone. Terminal line obsolete, fine, whitish or rosy-pinkish, defined with tiny blackish dots between veins and with a few whitish scales around these dots. Cilia strongly variegated, rosy-orange or pinkish, striolate with darker grey and blackish. Hindwing shining, pale rosy-pinkish with metallic ochreous brilliance, inner area with weaker or stronger dark greyish irroration. Discal spot small, diffuse but clearly visible, transverse line and submarginal stripe diffuse, interrupted, dark fumous grey. Veins partly covered with dark grey-brown; terminal line dark brown at upper two-third, pinkish at tornus; cilia pale rosy-pinkish or rosy-brownish, with a few darker brown-grey scales, especially at termen. Underside of forewing brilliant ochreous-whitish, suffused with dark greyish brown, costal and apical areas irrorated with pinkish-rosy scales. Crosslines and stigmata generally absent but traces of upperside markings recognisable as pale ghosts. Underside of hindwing much paler, milky whitish with weaker greyish and stronger rosy suffusion, especially in costal and apical areas. Discal spot rather sharply defined, rounded, transverse line diffuse but clearly visible, both markings dark greyish brown.

Male genitalia (Fig. 21): The general characterization of the male genital capsule is given under the Diagnosis of the genus (see above), the characteristic features of the new species as as follows: Valvae slightly asymmetrical with weak pyramidal subapical prominence on dorsal side of right cucullus; apical part of valva strongly tapering into acute, horn-like apical part of cucullus, corona absent; ampulla long, strong, more or less falcate; clavus lobate, large; apical part of sacculus with strongly sclerotized plate; ventral edge of sacculus terminated in small, triangular lobe; basal tube of vesica with two serrate ventro-lateral bars; apical cornutus of frontal diverticulum relatively large; subterminal diverticulum projecting slightly backwards and ventro-laterally; terminal part of vesica rather straight, directed proximally.

Female genitalia (Fig. 25): Ovipositor short, weakly sclerotized, truncated conical, papillae anales small, quadrangular; gonapophyses slender, fine. Ostium and ductus bursae heavily sclerotized, flattened, forming a firmly fused complex. Ostium quadrangular broad and rather short, without caudal incision; ductus broadly tubular, posterior third dilated, broader than ostium, with convex lateral margins, anterior third tapering towards junction to bursa, its lateral margins upturned dorsally. Cervix bursae large, discoidal-globular, its junction to ductus bursae with short but strong, sclerotized crest. Apical part of cervix bursae with large, rounded, heavily sclerotized subapical patch nearby origin of ductus seminalis, basal part with large, proximo-lateral sclerotized area. Corpus bursae elliptical-sacculiform, with rugose, somewhat neck-like posterior quarter, main part of corpus with four inequal, ribbon-like signa.

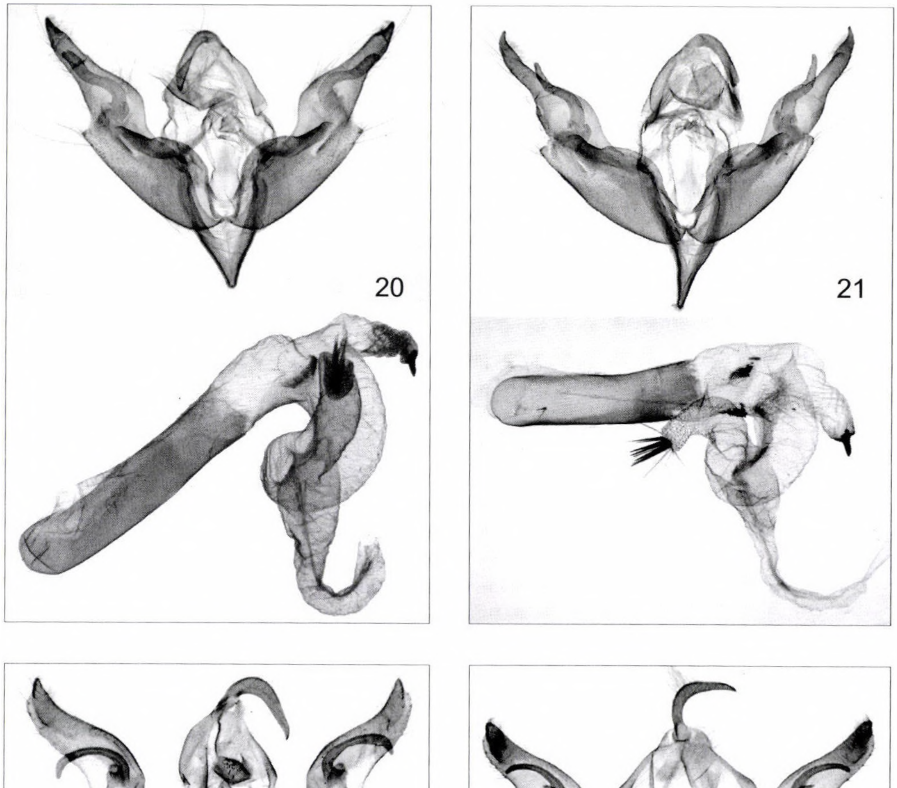
Diagnosis. The new species differs externally from its sister species, *O. knyvetti* by it more unicolorous, darker forewing colouration with weaker, finer, less



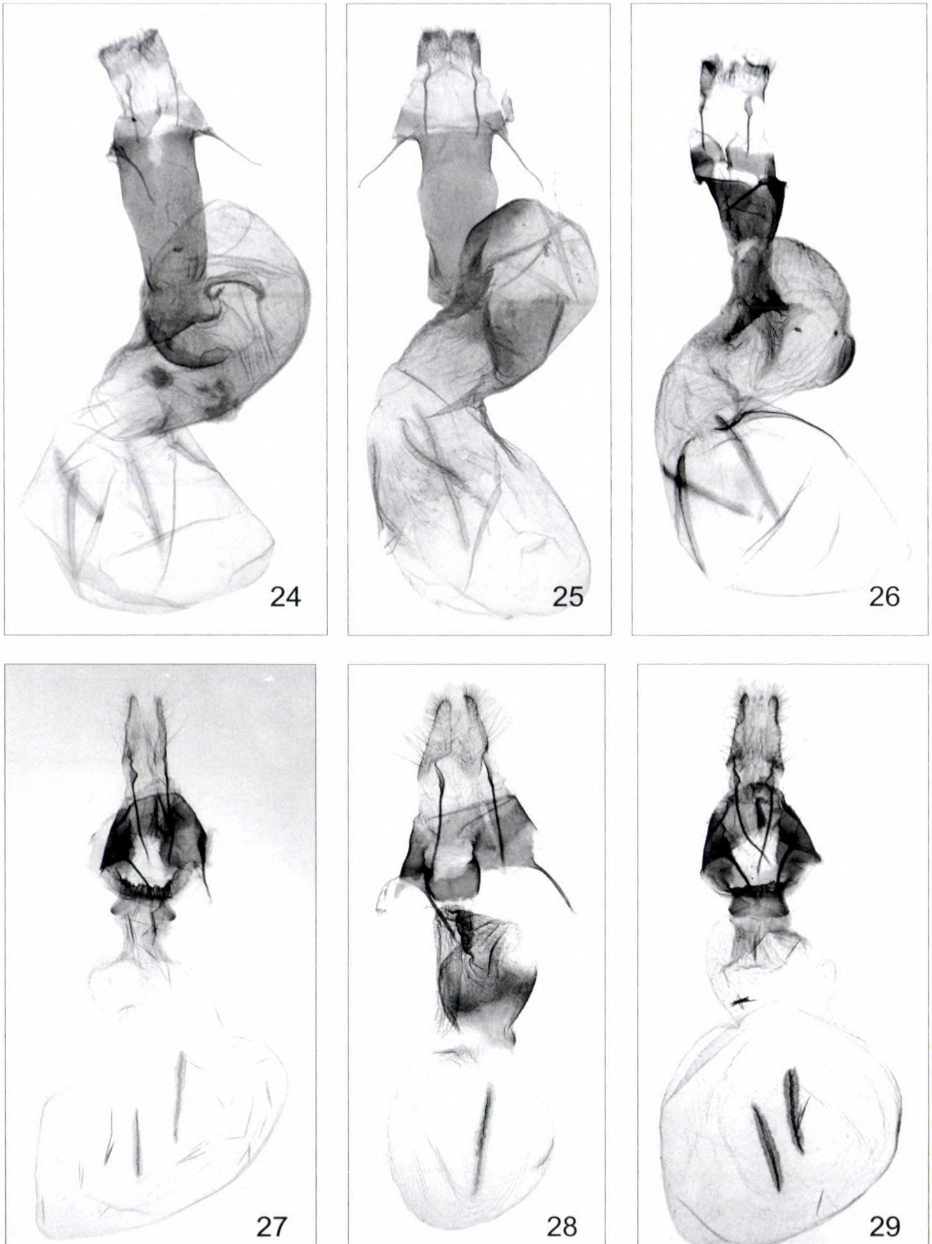
Figs 9–16. 9 = *Egiropolia kingmana* sp. n., holotype, male; 10 = *Dryobotodes caerulescens* sp. n., holotype, female; 11–12 = *Potnyctycia nemesi* sp. n.: 11 = holotype, male, 12 = paratype, female; 13–14 = *P. taiwana* CHANG: 13 = male, 14 = female; 15–16 = *Taeneremina scripta* sp. n.: 15 = holotype, male, 16 = paratype, female



Figs 17–19. Genitalia apparatuses. 17–18 = *Anorthoa changi* sp. n.: 17 = male genitalia, paratype, 18 = female genitalia, holotype; 19 = *Egiropolia kingmana* sp. n., male genitalia, holotype



Figs 20–23. Male genitalia of *Orthopolia* species: 20 = *O. knyvetti* HAMPSON, Nepal, 21 = *O. scotoptera* sp. n., paratype, 22 = *O. tayal* YOSHIMOTO, Taiwan, 23 = *O. gonggashana* sp. n., holotype



Figs 24–29. Female genitalia. 24–27 = *Orthopolia* species: 24 = *O. knyvetti* HAMPSON, Nepal, 25 = *O. scotoptera* sp. n., paratype, 26 = *O. tayal*, Taiwan. 27–29 = *Dryobotodes* species: 27 = *D. caerulescens* sp. n., holotype, 28 = *D. formosanus* HREBLAY et RONKAY, Taiwan, 29 = *D. intermissa* BUTLER, Taiwan

conspicuous whitish definition of the crosslines and the outlines of the stigmata, the smaller, more rounded orbicular stigma, the longer, more sharply defined black patch of the basal dash, the finer, almost continuous, medially less waved subterminal line and the more crenulate cilia; the hindwing of *O. scotoptera* is somewhat darker, more pinkish than that of *O. knyvetti*. The forewing colouration of *O. scotoptera* is conspicuously darker than that of *O. tayal*, without the intense pale pinkish suffusion of the basal and marginal areas being characteristic of *O. tayal*, the suborbicular patch is shorter, more diffuse, brownish or ochreous grey, not prominently white and long as in *O. tayal*, the frontal tuft of hair is blackish (it is white in *O. tayal*), the filling of the stigmata is darker, etc. The forewing colouration of *O. scotoptera* and *O. gonggashana* are similarly dark but *O. scotoptera* has no prominent white subcellular streak (it is conspicuous, long in *O. gonggashana*), the inner half of the marginal area is paler, violaceous-pinkish (not dark plumbeous grey as in *O. gonggashana*) and the hindwing is characteristically rosy-pinkish suffused, with diffuse transverse stripe and submarginal band while the hindwing of *O. gonggashana* is whitish with broader greyish-brown suffusion in the marginal field.

The ground plan of the male genitalia of *O. scotoptera* and *O. knyvetti* is very similar, the configuration of the clasping apparatus of the *O. tayal–O. gonggashana* pair of species is rather different from those of the two congeners (see the description of the genus). The male genital capsule of *O. scotoptera* differs from that of *O. knyvetti* by its somewhat larger size, more elongate valvae with much weaker subapical prominence and longer, terminally curved, horn-like cucullus and by the somewhat longer, stronger ampulla. The structure of the aedeagus and the vesica of the two closely related species is more different as the basal tube of vesica of *O. scotoptera* has two serrate ventro-lateral bars (*O. knyvetti* has only one) and the apical cornutus of the frontal diverticulum is larger in the new species. The projection of the distal part of the vesica is also different in the two species, as the subterminal diverticulum of *O. scotoptera* is projecting slightly backwards and ventro-laterally and the terminal part of the main tube of the vesica is rather straight, directed proximally (towards the coecum penis). The subterminal diverticulum and the terminal part of vesica of *O. knyvetti* are situated ventro-laterally and projected slightly forward.

The specific differences between the three species of *Orthopolia* are more prominent in the female genitalia. The key feature of *O. scotoptera* is the presence of a large, heavily sclerotized apical (distal) plate of the cervix bursae which is supposedly homologous with the proximo-lateral, pouch-like, partly sclerotized appendage of the two other species (see Figs 24–26). The configuration of the ostium-ductus complex is also different in the three species, it is an entirely fused,

heavily sclerotized, flattened organ in the *O. knyvetti*–*O. scotoptera* species-pair while ostium and ductus bursae are less sclerotized and separated by a narrow membranous zone in *O. tayal*. The proportion of the ostium-ductus complex is different in *O. knyvetti* and *O. scotoptera*, the ostium of the new species is narrower, the posterior third of the ductus is broader than in *O. knyvetti*, therefore, the broadest part of this organ is the posterior end in *O. knyvetti* while it is the medial third in *O. scotoptera*. The medial incision of the caudal end of ostium bursae of *O. scotoptera* is weak or absent, it is well-developed in *O. knyvetti*. Finally, the proximo-lateral sclerotization of the cervix bursae is significantly stronger in *O. scotoptera*.

Bionomics and distribution. The species was found in two subsequent years in the highest forested areas of the Fansipan Mts, inhabiting different parts of the elfin forest zone. It is a characteristic member of the winter fauna, the first imagines appear at the very end of January, most specimens of the series found in the first days of February are very freshly emerged ones. The first known specimens of *Orthopolia scotoptera* were collected a year earlier in the lower part of the elfin forest belt in mid-March, when the specimens were rather worn. The species has not been recorded yet from the lower altitude primary forests of the Fansipan nor from the later spring period in its known habitats. All specimens were observed at light, a part of the material was collected by small, portable light traps operating with 6 W UV-tubes.

Etymology: The specific name refers to the dark forewing colouration of the species.

Remarks. The correct configuration of the vesica, according to its size, coiling and the large diverticula, can be easily studied during the preparation process but this configuration cannot be properly saved when covering the slide. Thus, the actual position of the different parts of the vesica mounted on a slide is always artificial in a certain degree and the photographs taken show also these artifacts.

Orthopolia gonggashana sp. n.
(Figs 8, 23)

Holotype: male, "CHINA, Sichuan, Gongga Shan, 2600-3200 m, 101°58'E, 29°41'N, 23.IV.–15.V.2001, leg. V. Siniaev & A. Plutenko"; slide No. RL7517 (coll. G. RONKAY, in HNHM Budapest).

Description. Wingspan 41 mm, length of forewing 18 mm. Head and palpi blackish, tips of palpi, a stripe between antennae, parts of vertex and collar white, latter mixed with ochreous-brown

hair-scales. Thorax deep coal-blackish, mixed with a few whitish scales, metathoracic tuft small but prominent, whitish and pale brown. Dorsum of abdomen ochreous-brownish, lateral ridges somewhat darker; dorsal crest well-developed, blackish brown; ventral side dark fumous grey except ochreous-brownish anal tuft. Forewing elongate, narrow, with apex pointed; ground colour rather unicolorous dark violaceous grey, irrorated with blackish scales, outer part of basal field, subcellular zone and inner half of marginal field suffused with dark plumbeous grey scales. Basal area broad, its costal part whitish, subbasal line represented by black dots followed by whitish patches; basal dash a short black patch. Median area constricted below cell; antemedial and postmedial lines indistinct, fine, black with whitish inner definition, former oblique, almost straight, latter arched at costa and along reniform stigma, lower half of it rather straight. Median fascia poorly visible, represented by a diffuse dark shadow. Orbicular stigma rounded, whitish, its centre ochreous-brownish; reniform rather large, bean-shaped, defined with fine black and whitish annuli, filled with ground colour. Claviform stigma rather obsolete, short, triangular, dark blackish grey. Suborbicular white streak conspicuous, long, narrow. Marginal area broad, inner part suffused with dark plumbeous grey; subterminal line fine, white, more or less continuous, less waved; termen with rounded whitish patch. Terminal line obsolete, fine, whitish, defined with tiny blackish dots between veins. Base of cilia blackish, chequered with whitish. Hindwing shining ochreous-whitish, irrorated with darker grey-brown scales; veins finely brownish. Discal spot small, diffuse but clearly visible, transverse line partly obsolete, shadow-like; marginal area suffused with dark fumous grey, especially at tornal area. Terminal line dark brown, cilia whitish, dotted with brown. Underside of wings brilliant ochreous-whitish, forewing strongly suffused with dark grey; traces of upperside markings recognisable as pale ghosts. Costal and apical parts of hindwing also strongly irrorated with greyish, discal spot and transverse line rather sharply defined, dark greyish brown.

Male genitalia (Fig. 23): Uncus short, slender, tegumen weak, penicular lobes rounded; fultura inferior more or less trapezoidal. Valvae elongate, symmetrical, medially curved, ventral margin rather S-shaped. Distal half of valva relatively broad, less sclerotized, evenly tapering into acute, triangular cucullus; corona present, short, weak. Sacculus elongate, sclerotized, clavus reduced; dorsal edge with fine, weak triangular process. Basal plate of harpe with fine postero-lateral process, apical (erect) part short, acutely triangular. Ampulla long, slender, falcate. Aedeagus rather long, cylindrical, straight, carina with weak ventral plate, lateral bar present, strongly serrate, extending into basal part of vesica. Frontal (subbasal) diverticulum tubular, with small, conical apical cornutus, subterminal diverticulum long, tubular, terminated in a large bundle of long, fine, pin-like cornuti.

Diagnosis. *Orthopolia gonggashana* sp. n. is the allopatric sister species of *O. tayal*. The comparison of the four species belonging to the genus are given under the Diagnosis of *O. scotoptera*, and the differences between the male genitalia of the two species-pairs are discussed in detail in the diagnostic part of the new genus. The male genitalia of *Orthopolia gonggashana* differ conspicuously from those of *O. tayal* by the features of the aedeagus and the vesica. The aedeagus of *O. gonggashana* is considerably longer, without stronger, nail-shaped sclerotization at the ventral end of the carina which is typical for *O. tayal* but with a long, serrate lateral bar extending into the basal part of vesica which is absent in *O. tayal*. The basal part of the vesica of *O. tayal* is armed with two groups of long spinules, these bundles of cornuti are missing from *O. gonggashana*. Finally, the distal, tubular diverticulum of *O. gonggashana* is longer than that of the sister species, and is armed

with somewhat longer, pin-like cornuti. The clasping apparatuses of the two species are very similar in their ground plan but the uncus of the new species is slenderer, the valva is less curved medially, the ampulla is finer, shorter and the harpe is apically more acute than those of *O. tayal*.

Bionomics and distribution. A poorly known species, the unique specimen was collected at the medium high altitude forest zone of the Gongga Shan massif, at the end of the spring.

Etymology: The specific name refers to the type locality of the species.

Egiropolia gen. n.

Type species: *kingmana* sp. n.

Diagnosis. The new genus belongs to the tribe Orthosiini, its supposedly closest related genera are the members of the *Egira* DUPONCHEL, 1845 – *Orthopolia* gen. n. – *Lithopolia* YOSHIMOTO, 1993 – *Xylopolia* SUGI, 1982 generic complex. *Egiropolia* is, as yet, monotypical, its type species is known from a small island between Taiwan and the continental China.

The type species of the genus shows the strongest superficial resemblance with the taxa of the *Xylopolia bella* (BUTLER, 1881) species group and partly with the *Egira saxea* (LEECH, 1889) – *E. acronyctoides* (WILEMAN, 1914) species pair but differs from them by several genital and certain external features.

The diagnostic characteristics of the genus are as follows: Frons smooth, with dense, prominent tuft, palpi very short, third segment tiny, short, being considerably shorter than those of *Xylopolia* and *Clavipalpula* STAUDINGER, 1892. Male antenna filiform, loosely fasciculate with short cilia; tegulae rather distinct, pro- and metathoracic tufts large; abdomen long, slender, with well-developed lateral ridges and anal tuft but with weak dorsal crest; basal abdominal coremata absent. Male genital capsule large, sclerotized; uncus flattened, tongue-shaped; tegumen short, narrow, penicular lobes fine, ribbon-like. Valvae symmetrical, elongate, with more or less parallel margins, costa with small, acutely triangular subapical lobe; cucullus small, triangular, with short digitiform apical process and small, rounded pollex-like lobe; corona absent. Ampulla strong, rather slender, falcate, situated distally; harpe reduced to its flattened, apically acute basal plate. Aedeagus long, thick, cylindrical, distal part curved ventrad; carina with long, broad, sclerotized dorso-lateral plate; vesica long, broadly tubular, entirely membranous, with basal and medial diverticula but without cornuti or cornuti field.

The male genitalia of *Egiropolia* (Fig. 19) differ from those of all related genera (*Egira, Orthopolia, Kisegira* HREBLAY et RONKAY, 1999, *Lithopolia, Xylopolia, Clavipalpula*) by the features of the aedeagus and the vesica: the aedeagus of *Egiropolia* is stronger, thicker, distally strongly curved, with broad, large dorsolateral plate of the carina, the vesica is long, broadly tubular, not helicoidal or bifid, lacking any cornuti or cornuti field(s). The male genital capsule differs from that of *Egira* (see e.g. HREBLAY & RONKAY 1999, Figs 35–40, 64, 65) by its symmetrical valvae with more or less parallel costal and ventral margins but without narrower neck below cucullus (*Egira* may have distally evenly tapering valva terminated in acutely pointed apex), the presence of a subapical costal extension, the reduced pollex and corona, the more distally situated ampulla, etc. It can be distinguished from that of *Lithopolia* (see e.g. HREBLAY & RONKAY 1999, Figs 62, 63, 66–70) by its basally broader valvae, without corona and large setose surface of cucullus, reduced pollex, larger, more distal ampulla, much larger fultura inferior, etc.; from those of *Xylopolia* and *Clavipalpula* (see e.g. KONONENKO & RONKAY 1995, Figs 7–20) by the strongly dissimilar valval shape with much smaller cucullus, without corona but with costal extension, apical process and rounded pollex, the considerably shorter, broader uncus, the less developed penicular lobes, the larger fultura inferior, the more distally situated ampulla, etc. The comparison of the male genitalia of *Egiropolia* and *Orthopolia* are given in the diagnosis of *Orthopolia*.

The detailed description of the external and genital features of the type species is given below, its diagnostic characters, besides the unusually colourful forewing, are the same as those of the generic ones.

Distribution. Endemic to the island Kingman (Taiwan).

Egiropolia kingmana sp. n.
(Figs 9, 19)

Holotype: male, [Taiwan], "Kingman, FUJEAN, IV–16–1993, Y. B. Fan"; slide No. RL7091 (coll. TFRI, Taipei).

Description. Wingspan 39 mm, length of forewing 18 mm. Head large, frons broad, with dark brownish tuft; palpi laterally dark brown. Collar and tegulae dark violaceous brown, pro- and metathoracic tufts whitish-greyish. Abdomen long, robust; dorsal side pale ochreous-brownish with a few greyish hairs, dorsal crest reduced to a small dark grey basal tuft. Lateral ridges and anal tuft long, pinkish-rufous; ventral side dark red-brown. Basal abdominal coremata absent. Forewing elongate, relatively broad, with apex pointed; outer margin finely crenulate. Colouration of forewing rather variegate, ground colour dark brown, irrorated with dark greyish and whitish scales. Lower half of basal area, median field below cubital vein and apical part suffused with pale reddish brown,

costa with dark ashy grey scales; filling of orbicular and large patches at tornus and below medial veins fine silvery greyish, filling of reniform stigma and outer area of cell pale orange-pinkish. Cross-lines rather indistinct, subbasal, antemedial and postmedial lines fine, simple, sinuous, black(ish) with weak whitish definition; median fascia deleted. Outlines of orbicular and reniform stigmata incomplete, fine, blackish; claviform stigma absent. Subterminal line obsolete, veins with weak blackish covering in outer half of wing; terminal line a row of small blackish triangles; cilia as ground colour. Hindwing shining, milky ochreous white, discal spot small, diffuse but clearly visible, transverse line absent. Marginal area with weak brownish irroration, veins also brownish in outer third of wing. Terminal line brown, cilia also pale brownish. Underside of forewing suffused with brown, small, rounded discal spot and broad, diffuse transverse line even darker, clearly visible, trace of subterminal line also recognisable. Underside of hindwing shining milky white, costal and apical parts irrorated with red-brown. Discal spot sharply defined, rather rounded, transverse line a row of dark spots on veins.

Male genitalia (Fig. 19): Genital capsule large, sclerotized, valvae about as long as aedeagus. Uncus medium-long, flattened, narrowly tongue-shaped, with strong but relatively short postero-lateral setae on ventral surface. Tegumen short, narrow, penicular lobes fine, ribbon-like. Fultura inferior sclerotized, more or less subdeltoidal, with fine medio-apical incision; vinculum strong, long, V-shaped. Valva elongate with more or less parallel margins from base towards small, acutely triangular subapical costal lobe. Cucullus small, rather triangular, with short but strong, digitiform apical process and very short, rounded, lobate ventral extension ("pollex"). Corona absent, ventral surface of cucullus finely setose. Sacculus relatively long, broad, terninated in flat, triangular distal extension; clavus reduced. Editum small, weak, sparsely setose; ampulla strong, rather slender, falcate, with pointed apex; harpe represented by its flattened, apically acute basal plate. Aedeagus long, thick, cylindrical, distal third curved ventrad; carina with long, broad, sclerotized dorso-lateral plate, armed with a few small teeth, and with a much shorter ventro-lateral bar. Vesica long, broadly tubular, everted ventrally, curved postero-laterally, distal end upturned dorsally. Walls of vesica entirely membranous, basal part with large, flat, subconical diverticulum, medial part with two large pocket-like diverticula, one of them covered with minute spiculi; distal part of vesica strongly tapering, narrowly tubular.

Bionomics and distribution. The species is known only by its unique holotype which was collected at light at the early spring. No additional information about its bionomics is given.

Etymology: The specific name refers to the home island of the species.

Dryobotodes caerulescens sp. n.
(Figs 10, 27)

Holotype: female, "Taiwan, Prov. Taitung, Yu-Shan Mts, Yakou, 2600 m, 1–3.XI.1996, leg. Gy. Fábián and F. Nemes", slide No. RL6290 (coll. GY. FÁBIÁN, in HNHM Budapest).

Diagnosis. The new species is the allopatric sister taxon of *Dryobotodes intermissa* (BUTLER, 1886). It differs externally from the more northern Pacific twin species by its lighter, more bluish-greyish colouration of the outer part of the

forewing, the presence of small mossy green patches in the basal and medial fields (they have been faded into yellowish since the time of collecting), and by the much paler inner area of the hindwing, respectively. The female genitalia of *D. caerulescens* are similar in type to those of its close relative (see Figs 27–29) but the ostium bursae of the new species is narrower and longer, more dilated proximally, the ductus bursae is slightly longer and the two signa in the corpus bursae are strongly inequal (one of them is almost twice as long as the other one, those of *D. intermissa* are equal in length). In addition, the incision of the last sternite is much deeper, more V-shaped in case of *D. caerulescens*.

Dryobotodes caerulescens resembles also *D. formosanus* HREBLAY et RONKAY, 1998 (see also HREBLAY & RONKAY 1997; HREBLAY *et al.* 1999) but the forewings are more bluish-greyish, without intense mossy green suffusion, and the hindwing of the new species has a well-marked discal spot on both surfaces which is obsolete or deleted in *D. formosanus*. The female genitalia of the two species are easily distinguishable as the caudal margin of the ostium bursae is cristate-crenulate in the new species but simple, smoothly sclerotized in *D. formosanus*. The ostium and the ductus bursae are broader than those of *D. formosanus*, the appendix bursae is membranous in *D. caerulescens* while it is strongly scobinate and partly sclerotized in *D. formosanus* and the latter species has not two but three signa. The last sternite of *D. formosanus* has only a small, shortly V-shaped caudal incision, this incision is much stronger, deeper in the *D. caerulescens–D. intermissa* species pair.

Description. Wingspan 34 mm, length of forewing 15 mm. Female. Head and thorax strongly variegated, dark grey, mixed with blackish, mossy green, ochreous and white hair-scales; collar and tegulae marked with blackish lines; thoracic tufts large, greyish with whitish tip. Palpi short, upturned, laterally blackish; antenna filiform, shortly, sparsely ciliate, dorsal surface covered with white scales. Forewing elongate, narrow, with apex pointed; outer margin obliquely arcuate, slightly crenulate. Wing pattern strongly variegated with differently coloured small patches ans darker and paler elements of noctuid maculation; scaling finely reticulate. Basal and medial areas dark olive-brownish, with with bluish ash-grey, mossy green, black and white irroration and with small mossy green patches and a larger pale grey patch at inner margin. Basal area broad, median field strongly constricted below cell. Subbasal, antemedial and postmedial lines rather indistinct, simple, sinuous, blackish, defined with pale gray and whittish scales; upper part of median fascia broad, diffuse, blackish. Orbicular stigma small, ovoid, with pale darker grey outline and whittish filling with dark greay centre. Reniform stigma large, incompletely encircled with blackish, filled with whittish, dark grey and orange-ochreous scales; claviform stigma an incomplete blackish circle with brownish filling. Suborbicular stigma conspicuous, oblique, white, surrounded with diffuse black zone at lower half. Marginal area rather broad, suffused with light, bluish ash-grey; subterminal line whitish, fine, sinuous, defined by broad whitish-grey stripe and orange-brownish irroratation at inner side, and by a few blackish grey dots and brownish patches outwards. Terminal line a row of blackish triangles; cilia ochreous grey, spotted with whitish and dark brown dots. Hindwing shining whitish, suffused with brown, veins and rather broad marginal area darkened; discal spot a diffuse, narrow, brownish

lunule. Terminal line dark brown, cilia whitish with dark brown line and outer spots. Underside of forewing suffused strongly with dark brownish grey, discal spot marked by a fine, darker lunule. Hindwing whitish, costal and marginal areas covered with dark brownish grey; discal spot small but strong, upper part of transverse line diffuse but easily recognizable.

Female genitalia (Fig. 27): Ovipositor relatively long, conical, papillae anales elongate, with apex pointed; apophyses posteriores long, slender, a. anteriores somewhat shorter, also fine. Ostium bursae more or less trapezoidal, sclerotized on both surfaces, dilated proximally, caudal margin strongly cristate and crenulate, fused with similarly cristate-crenulate ventral edge of lamina antevaginalis. Ductus bursae short, rather broad, flattened, gelatinous and weakly scobinate, appendix bursae small, membranous, with globular lateral pouch at right side. Corpus bursae ellipsoidal, weakly membranous, with two signum-stripes, a longer ventral and a much shorter dorsal one.

Bionomics and distribution. Poorly known, the unique type specimen was collected at light, in the late autumn in the highest, rather scattered deciduous forest zone, mixed with conifer woodland patches and rocky grassland vegetation on the steep slopes.

Etymology. The specific name refers to the bluish grey forewing ground colour of the species.

Potnyctycia taiwana (CHANG, 1991), **comb. n.**
(Figs 13, 14, 31, 34)

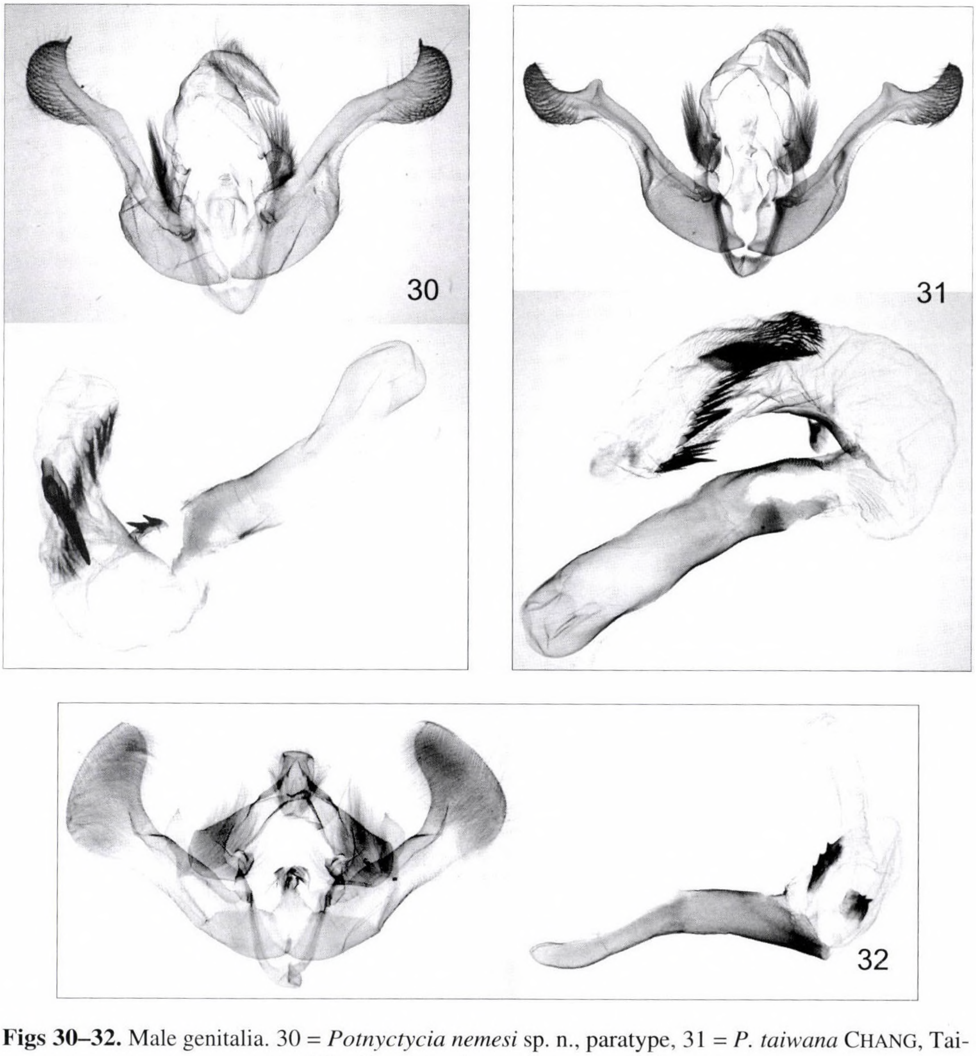
Material examined. Taiwan. Prov. Taoyuan: 3 males, 1 female, 16 km E of Fuhsing, 900 m, 121°27'E, 24°50'N, 30.XI.–1.XII., 14.XII.1997, leg. S. SIMONYI & A. SZABÓ; Prov. Taitung: 3 males, 3 females, Hsiangyang, Police station, 2320 m, 25–26.X. and 2.XI.1996; 1 male, 2 km N Liyusan, 1760 m, 23.X.1996, leg. GY. FÁBIÁN & F. NEMES. Prov. Ilan: 21 males, 37 females, Ming Chyr Forest Recreation Area, 1160 m, 10–11.XII.1997. leg. GY. FÁBIÁN; 2 males, 1 female, from the same site, 27–28.XI.1998, leg. GY. FÁBIÁN & Z. KORSÓS. Prov. Hualien: 3 males, 4 females, Taroko valley, 2000 m, 3–5.XII.1998, leg. GY. FÁBIÁN & Z. KORSÓS (coll. HNHM, FÁBIÁN, HREBLAY and G. RONKAY).

Slide Nos HM10135, HM10163, HM10169, HM10170, RL6565, RL6566 (males), HM10136, HM10171, RL6567 (females).

Taxonomic comments. The species was originally placed into the genus *Antivaleria* SUGI, 1980 by CHANG, the numbers of the genitalia figures of this species and that of *Meganephria "extensa* Butler" (= *M. crassa* OWADA et Kobayashi, 1996) had changed in the original description (CHANG 1991: figs 125 and 129). The studies of large series of "*A. taiwana*" revealed the fact that there are two, partly sympatric, species which are hardly separable by their external features but are easily distinguishable by the male genitalia. As the holotype of the species has not been dissected and the fig. "129" illustrates the genitalia of the male paratype, subsequent study of the holotype of *P. taiwana* (in NMNS, Taichung) proved that the male genitalia having acute spine of the valval apex and less developed

subapical costal lobe should be considered as an undescribed *Potnyctycia* (see also HREBLAY & RONKAY 1997, Figs 87–88 as "*Atrachea taiwana*") while the genitalia of the true *P. taiwana* have remained as yet unpublished.

These two species represent a rather distinct species-group within the genus *Potnyctycia* HREBLAY et RONKAY, 1997, both are endemic to Taiwan. They differ relatively strongly from the other congeners (see HREBLAY & RONKAY 1997, 1998) by their external appearance but the configuration of the genitalia of both



Figs 30–32. Male genitalia. 30 = *Potnyctycia nemesi* sp. n., paratype, 31 = *P. taiwana* CHANG, Taiwan, 32 = *Taeneremina scripta* sp. n., holotype

sexes inevitably show their close relationship with the *P. obsoleta* HREBLAY et RONKAY, 1998 – *P. cristifera* HREBLAY et RONKAY, 1997 – *P. frontieri* HREBLAY, PEREGOVITS et RONKAY, 1999 species-group.

Redescription of the male genitalia (Fig. 31): Uncus strong, lanceolate, dorsally flattened, apex finely rounded. Tegumen rather broad, penicular lobes narrow, long, densely setose. Fultura inferior sclerotized, subdeltoidal, vinculum very short, strong, more or less V-shaped. Valva long, narrow, finely curved, medially strongly constricted. Subapical costal lobe well-developed, rounded triangular, cucullus large, foot-shaped, with apex rounded, covered with strong setae. Sacculus rather short, clavus rounded triangular, sclerotized, finely covered with sensory setae. Harpe reduced to its short, slender basal bar, ampulla absent. Aedeagus long, cylindrical, curved at middle, carina with sclerotized, eversible dorsal and ventral bars. Vesica broadly tubular, everted forward, recurved dorsally. Basal half inflated, inner curve with long, narrow sclerotized plate and with small, nail-head-shaped basal cornutus laterad. Medial part with strong, bulbed, thorn-like cornutus having large, elongate basal plate, distal half with long field of strong, spiniform cornuti on opposite surface.

The female genitalia (Fig. 34) are very similar to those of *P. nemesi*, the description of which is given below (see Fig. 33), but the anterior part of the ductus bursae is more dilated, the sclerotized, folded right margin is somewhat shorter, the caudal margin of ostium bursae is with narrower, shallower incision and the sclerotized, cristate-ribbed medial plate of the appendix bursae is longer, more curved posteriorly towards ductus bursae.

Potnyctycia nemesi sp. n.
(Figs 11, 12, 30, 33)

Holotype: male, "Taiwan, Prov. Hualien, Taroko valley, 2000 m, 3–5.XII.1998, leg. Gy. Fábián & Z. Korsós" (coll. GY. FÁBIÁN, deposited in HNHM, Budapest).

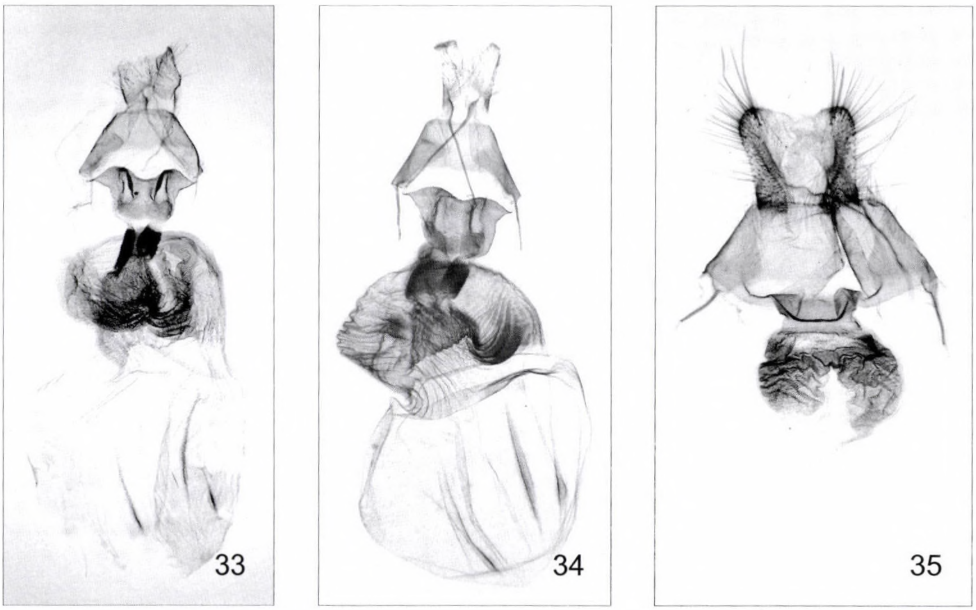
Paratypes: Taiwan. Prov. Hualien: 2 males, 4 females, with the same data as the holotype. Prov Taichung: 3 females, 35 km E of Tungshih, 2020 m, 6. and 13.XII.1997, 120°50'E, 24°19'N; 2 males, 50 km E of Tungshih, 2500 m, 19.XII.1997, 120°55'E, 24°19'N, leg. S. SIMONYI & A. SZABÓ. Prov. Nantou: 1 male, 3 km SW of Tsuifeng, 2100 m, 18.XII.1997, 121°10'E, 24°06'N, leg. S. SIMONYI & A. SZABÓ; 1 male, Wushe, 28–29.XII.1994, leg. LIN and YANG; 1 male, paratype of *A. taiwana* (its genitalia are figured by CHANG 1991, Fig. 129) (coll. NMNS Taichung, HNHM, FÁBIÁN, HREBLAY and G. RONKAY).

Slide Nos HM10143, RL5768, RL7138 (males), HM10166, RL7139 (females).

Diagnosis. The new species is hardly distinguishable externally from its closest relative, *P. taiwana* (CHANG, 1991) although the greenish pattern of the forewing of *P. nemesi* sp. n. is paler, grass-greenish, without stronger dark olive-greenish irroration and the last sternite of the female is larger, wider, with broader, V-shaped caudal incision. The genitalia of both sexes show, however, easily recognizable differences (see Figs 30, 31, 33, 34; also CHANG 1991, Fig. 129; HREBLAY & RONKAY 1997, Figs 87, 88). The male genitalia of the new species differ conspicuously from those of *P. taiwana* by their much smaller, often fully reduced

subapical costal lobe and the presence of the acute apical spine of the cucullus, the broader, pentagonal, rather shield-like fultura inferior and the smaller clavus. In the female genitalia the posterior and anterior parts of ductus bursae are more or less equally broad in case of the new species, with longer sclerotized, folded right lateral margin and the sclerotized plate of appendix bursae is shorter, posteriorly less curved than in *P. taiwana*.

Description. Wingspan 36–39 mm, length of forewing 17–19 mm. Male. Pubescence of head and thorax dark olive-green, abdomen paler, more greyish. Antenna filiform with dense cilia. Forewing elongate with apex pointed, outer margin finely crenulate. Ground colour bright, rather dark mossy green, medial area and outer half of marginal field with variably strong dark brownish suffusion. Subbasal, ante- and postmedian crosslines indistinct, double, filled with paler green, median fascia diffuse, sinuous, dark brown. Orbicular stigma slightly flattened, oblique, reniform larger, elliptical, both encircled with blackish and green annuli, filled with darker greyish, claviform represented by diffuse, dark brown arch. Subterminal line fine, sinuous, rather indistinct, whitish green, defined with darker brown outer shadow. Terminal line consisting of a series of small blackish lunules, cilia as ground colour. Hindwing uniformly dark greyish brown, discal spot obsolescent, narrow, lunulate, terminal line darker brown, cilia paler ochreous brown with darker medial line. Underside of wings pale ochreous grey, most part of forewing suffused with dark grey-brown, discal spot of hindwing strong, transverse line more diffuse but well discernible. Female. Similar to male, antenna shorter with finer cilia. Last sternite with deep, broad, rather V-shaped caudal incision.



Figs 33–35. Female genitalia. 33 = *Potnyctycia nemesi*, paratype; 34 = *P. taiwana* CHANG, Taiwan, 35 = *Taeneremina scripta* sp. n., paratype

Male genitalia (Fig. 30): Similar in type to those of *P. taiwana* but having somewhat more elongate valvae with less concave costal margin of cucullus, with prominent, acute apical spine and reduced or entirely missing subapical costal lobe. Fultura inferior somewhat shorter, basally broader, more pentagonal; clavus smaller, rounded.

Female genitalia (Fig. 33): Ovipositor conical, medium-long, papillae anales elongated, weakly sclerotized, gonapophyses long, slender. Ostium bursae broad, medium-long, sclerotized, more or less lyriform, with deep, U-shaped caudal incision and arcuate, terminally pointed postero-lateral edges. Ventral plate significantly larger, stronger, with two prominent, broad longitudinal crests; dorsal surface of ventral plate densely covered with fine teeth. Ductus bursae short, proximal and distal parts more or less equal in width, sclerotized lateral margins upturned, folded, being longer on right side. Appendix bursae bilobate, postero-lateral ventral (left) lobe small, globular-discoidal, finely ribbed and sclerotized, dorsal lobe larger, ribbed and wrinkled, with strongly sclerotized, ribbed-cristate medial plate. Corpus bursae ample, discoidal-globular, with subconical lateral section at right side. Walls of corpus bursae membranous, with long wrinkles and four fine, inequal signum-stripes.

Bionomics and distribution. *P. nemesi*, similarly to the other taxa of the genus, is a typical member of the late autumnal and winter fauna, the imagines are on wing from the beginning of December probably until the end of January. The two sister-species, *P. nemesi* and *P. taiwana* occur sympatrically and syntopically in the higher mixed forest zone of the central part of the eastern massif of the island. In addition, *P. taiwana* appears as rather frequent in the medium-high, humid deciduous and mixed forests in the northern mountainous areas of Taiwan.

Taeneremina gen. n.

Type species: *scripta* sp. n.

Diagnosis. The new, as yet monotypical, genus is rather remote from all known Ipimorphinae genera, the slight resemblance of the forewing markings of the type species of the genus with *Taeneremа hoenei* DRAUDT, 1950, is superficial, the structure of the body, the colouration of the forewing and the genitalia of the two species are conspicuously different. Certain features of the genitalia, especially the configuration of the vesica and the ostium and ductus bursae, but also the valval shape with the broad, densely hairy cucullus with long corona show its relationships with numerous Apameini genera. On the other hand, the complete lack of the ampulla and the costal extension ("digitus"), the well-developed, sclerotized harpe, the absence of the strong setae from the hairy zone of the cucullus and the structure of the ovipositor with the weak, apically rounded papillae anales (not being acute, conical, sclerotized, as in most Apameini taxa), without the two sclerotized bars from between papillae (the presence of whose is one of the most

important diagnostic features of the majority of Apameini females) clearly indicate the early segregation of the genus from the other genera of Apameini.

The detailed morphological characterization of the genus is given under the description of the type species.

Distribution. Endemic to Taiwan.

Taeneremina scripta sp. n.
(Figs 15, 16, 32, 35)

Holotype: male, "TAIWAN, Prov. Nantou, Tayuling, 2550 m, 7–8.X.1996, leg. Gy. Fábián and F. Nemes", slide No. RL6331 (coll. GY. FÁBIÁN, in coll. HNHM, Budapest)

Paratypes: Taiwan. Prov. Nantou: 2 males, 1 female, Piluchi, 14.IX.1986, leg. Y. C. CHANG, (coll. TFRI, Taipei). Prov. Taichung: 1 male, Anmashan, 2275 m, 13.IX.1996, leg. et coll. C. M. FU (Taiping).

Slide No. RL7077 (female).

Description. Wingspan 37–41 mm, length of forewing 17–18 mm. Sexes similar. Head large, frons broad, smooth, eyes large, globular, proboscis well-developed, palpi short, slender, upturned, third segment short, fine. Basal two-thirds of male antenna bipectinate with rather long, asymmetrical pectination, apical third filiform; female antenna entirely filiform. Pubescence of head and thorax rather homogeneous, long, scale-like, deep claret-red, mixed with whitish-ochreous and dark brown hair-scales; legs strong, tibiae without spines, tarsi with three rows of spines. Abdomen paler than thorax, dark ochreous brown, with well-developed dorsal crest basal abdominal coremata present. Forewing elongate, relatively broad, with finely pointed apex and arcuate, finely crenulate outer margin. Ground colour deep claret-brown or porphyreous brown, with fine violaceous shade, basal field and tornal area with ochreous irroration. Forewing pattern sharply defined, rather complex, all elements of noctuid maculation present; crosslines and stigmata marked with blackish brown and ochreous-whitish scales. Basal area broad, basal dash very short; basal and subbasal lines simple, strongly waved, blackish defined with ochreous-whitish scales. Upper part of median area broad, lower half strongly constricted. Antemedial and postmedial crosslines strongly sinuous, partly double, broad, filled with whitish-ochreous and a few greyish scales, median fascia conspicuous, relatively narrow, blackish, darkest element of pattern. Orbicular stigma small, round; reniform long, narrow, lunulate, both stigmata encircled with black-brown, filled with whitish-ochreous, reniform with pale brownish inner lunule. Claviform stigma large, larger than orbicular, encircled with blackish, filled with ground colour. Subterminal line whitish, strongly sinuous, defined with blackish brown patches and chevron-spots on both sides. Terminal line represented by a row of distinct, dark brown arches and spots; cilia as ground colour, finely chequered with whitish. Hindwing fuscous, with intense cupreous shining, marginal area darker brown, discal spot and transverse line obsolescent but recognizable. Terminal line deleted, cilia ochreous, spotted with brown. Underside of both wings rosy-ochreous, most parts of forewing and marginal area of hindwing suffused with dark brown. Transverse lines (one on forewing, two on hindwing) very broad, diffuse, dark brown stripes, traces of subterminal line also visible; discal spots present but not very conspicuous.

Male genitalia (Fig. 32): Uncus medium-long, flattened, spatulate, dorsally strongly hairy, apex obtuse. Tegumen very broad, penicular lobes large, quadrangular, densely hairy. Fultura infe-

rior subtriangular, dorsally tapering into strong, terminally finely rounded apical process; vinculum strong, V-shaped, with rounded tip. Valva elongate, basal two-third narrow, costa strongly sclerotized, ventral edge finely rugose. Cucullus very large, foot-shaped, rather narrow, densely hairy; corona long, relatively weak. Sacculus short, narrow, clavus represented by small, setose surface. Harpe strong, thick, flattened, lanceolate, with apex acute. Aedeagus cylindrical, short, slightly arcuate, ventral plate of carina elongate, beak-shaped with obtuse tip. Vesica rather short, inflated, membranous, armed with two strong, dentate plates ("cornuti"), ductus ejaculatorius projected dorsally.

Female genitalia (Fig. 35): Ovipositor shortly conical, papillae anales elongate, rather quadrangular, densely setose with long, fine setae, apophyses posteriores slender, relatively long. Penultimate segment medium-long, sclerotized, with fine apophyses. Ostium bursae short, rather broad, sclerotized, quadrangular, lateral margins slightly constricted at middle; ventral plate with deep medial depression. Posterior half of ductus bursae flattened, discoidal, both surfaces with intense verrucose sclerotization, arranged into flat, sinuous crests, ribs and folds, anterior half short, weakly membranous, tubular. Appendix bursae relatively small, elongate-subconical, entirely membranous; characters of corpus bursae unknown (the genitalia of the only known female specimen is broken below lower edge of appendix).

Bionomics and distribution. The known habitats of the species are montane, deciduous forest, above 2000 m altitude. It is presumably univoltine, the flight period, according to the data of the few known specimens, is September–October; the moths were collected at light.

Etymology: The specific name refers to the fine, rather complex forewing pattern.

*

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REFERENCES

BERIO, E. (1973) Nuove species e generi di Noctuidae Africane e Asiatiche e note sinonimiche. (Part II). *Annali del Museo Civico di Storia Naturale Giacomo Doria* **79**: 126–171.

CHANG, B. S. (1991) *Illustrations of Moths in Taiwan 5.* Taiwan Museum, Taipei, 366 pp.

DRAUDT, M. (1950) Beiträge zur Kenntnis der Agrotiden-Fauna Chinas. Aus den Ausbeuten Dr. H. Höne's. (Beitrag zur Fauna Sinica). *Mitt. münchn. ent. Ges.* **40**: 1–174.

HREBLAY, M., PEREGOVITS, L. & RONKAY, L. (1999) New genera and species of Noctuidae from Vietnam, Thailand and Nepal (Lepidoptera). *Acta zool. hung.* **45**(1): 1–96.

HREBLAY, M. & PLANTE, J. (1995) Description de sept especes nouvelles du Népal et d'un genre nouveau (Lepidopteres, Noctuidae). *Lambillionea* **95**: 135–144.

HREBLAY, M. & RONKAY, L. (1997) New Noctuidae (Lepidoptera) species from Taiwan and the adjacent areas. *Acta zool. hung.* **43**(1): 21–83.

HREBLAY, M. & RONKAY, L. (1998) Noctuidae from Nepal. *In* HARUTA, T. (ed.) *Moths of Nepal, Part V. Tinea* **15**(Suppl. 1): 117–310.

HREBLAY, M. & RONKAY, L. (1999) Neue trifide Noctuidae aus dem himalayanischen Raum und der südostasiatischen Region (Lepidoptera: Noctuidae). *Esperiana* **7**: 485–620.

KONONENKO, V. S. & RONKAY, L. (1995) On the Xylopolia species of the Manchurian Region (Lepidoptera, Noctuidae). *Acta zool. hung.* **41**(2): 119–129.

POOLE, R. W. (1989) *Lepidopterorum Catalogus* (New Series), Fasc. 118. E. J. Brill, Florida, 1314 pp.

RONKAY, G. & RONKAY, L. (2000) New Noctuidae taxa from Taiwan (Lepidoptera). *Bull. Nat. Mus. Nat. Sci.* **12**: 93–112.

RONKAY, L., YELA, J. L. & M. HREBLAY (2001) *Noctuidae Europaeae. Vol. 5. Hadeninae II.* Entomological Press, Sorø, 452 pp.

SUGI, S. (1955) A revision of the Japanese Orthosia (Lepidoptera, Noctuidae, Hadeninae). *Tinea* **2**(1–2): 90–104.

SUGI, S. (1982) Noctuidae. *In* INOUE, H. (ed.): *Moths of Japan, II.*, Plates and systematic catalogue. Kodansha, Tokyo, 552 pp.

SUGI, S. (1986) The Noctuidae of Taiwan 2. Genus Orthosia Ochsenheimer (Lepidoptera). *Ent. Pap. Pres. Kurosawa, Tokyo* **1986**: 98–105.

SUGI, S., M. OWADA & H. INOUE (1992) Noctuidae. *In* HEPPNER, J. B. & INOUE, H. (eds): *Lepidoptera of Taiwan, Checklist.* **1**(2): 171–202.

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